Native and invasive mammalian carnivores in a forestry and agricultural landscape in northwest Tasmania.

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Statement of Originality

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Joanna Lyall August 2017

Statement of co-authorship

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Joanna Lyall was the primary investigator and lead author. Chris Johnson, Sarah Munks and Menna Jones contributed to the idea, the study design and edited chapters.

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Joanna Lyall was the primary investigator and lead author. Chris Johnson, Sarah Munks and Menna Jones contributed to the idea, the study design and edited chapters.

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Ethics Statement

This study was conducted with ethics approval from the University of Tasmania Animal Ethics Committee Animal Ethics Committee, approval number: A13588, 6 November 2013.

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Our task must be to free ourselves by widening our circle of compassion to embrace all living creatures and the whole of nature and its beauty. Albert Einstein

Abstract

Globally, human activities including land clearing, habitat conversion and degradation, and human induced climate change are putting immense pressures on biodiversity. Habitat change is a primary cause of species decline and extinction, but in many places invasive predators, often favoured by habitat change, also have had large impacts on biodiversity through direct predation, competition and disease transmission.

In the Australian island State of Tasmania, a higher percentage of the original forest cover has been maintained than in other parts of Australia, retaining 63.8% of its c1750 forest cover, or 3.06 million hectares. Of this, following selective logging, clear-felling for regeneration or conversion to plantation species, approximately 25% of old growth forest remains. Land clearing for agriculture in Tasmania occurred particularly in the fertile country at lower altitudes, while forestry activities generally continued at higher elevations.

These changes to habitat affect the fauna differentially. In Tasmania, some mammal species such as the Tasmanian pademelon *Thylogale billardierii* appear to benefit from forest fragmentation and the introduction of exotic pasture species in proximity to refuge, however other species are likely to experience population decline through this loss of habitat. Within this fragmented landscape are the native marsupial predators, the Tasmanian devil *Sarcophilus harrisii* and spotted-tailed quoll *Dasyurus maculatus* and the introduced feral/domestic cat *Felis catus.* Recently, populations of the devil have declined by up to 85% because of Devil Facial Tumour Disease (DFTD), a lethal transmissible cancer that was first detected in 1996 and has spread across most of the island. Persecution of the devil and quoll still occurs. The cat became established throughout Tasmania following introduction at the time of European settlement and competes with the native carnivores in addition to carrying the disease, *Toxoplasmosis gondii*, to which many of the native herbivores are susceptible.

Few studies have examined in depth, the combination of available prey, landscape use and site level features determining whether devils, quolls or cats will use a particular site. Chapter 2 of this study aims to investigate further the way quolls, devils and cats are using this perturbed landscape, identifying the features at landscape and site level where each species is more abundant and relationships between the species. While Chapter 3 further analyses the use of plantations for new insights into the factors that influence the use of plantations by each species. Within a study area of approximately 250,000 ha in north-west Tasmania, I used camera survey data from 150 sites over two seasons to investigate the distribution and abundance of, and relationships between, the quoll, devil

and cat in relation to site and landscape factors within four land use categories. I used N-mixture modelling (Royle, 2004) with K=15 to estimate the direction and size of effect of the selected environmental parameters on the abundance of each predator species across the study area. As I was able to identify individual animals, I ran single species abundance models using the unmarked Point Count package "pcount", for both the winter and summer "seasons". This provides an estimation of abundance of each of the predators at each site.

Quolls and devils were more abundant at the same sites, and cats and devils had no adverse influence on each other's presence, however there was some evidence that quolls and cats avoid each other or choose different habitats. Quolls appeared to be more specialised in their habitat requirements than the other two species, with taller forests and understorey qualities influencing their occurrence, while elevation, forest cover and prey emerged as factors influencing the abundance of the devil. Cats were more abundant on the edges of agricultural land with this study indicating cover, including trees and undergrowth, is an important factor. Quolls and devils were less abundant in plantations than nearby forests while cats were more abundant in plantations in proximity to agricultural land. Differences between the species in where they were more abundant and relationships between species have been revealed by this study, however further study is required to determine the drivers. The relationship between cats and quolls should also be explored further to ascertain whether the negative relationship relates primarily to spatial influences or whether there is a temporal aspect to the relationship. Would interventions to increase understorey complexity in disturbed habitats reduce the spread and success of cats within the natural and plantation landscapes?

A more thorough investigation of potential den sites in plantations would be of value with a direct comparison with potential den sites in adjacent native forest. Further analysis of the abundance of different prey species and the diet of devils and quolls in plantations would be of interest in gauging the dietary flexibility of devils and quolls in plantations, seasonally and at different stages of the breeding cycle.

Quolls, devils and cats are coexisting within this fragmented landscape. Historical and current changes to the composition of the marsupial predator guild through loss of the thylacine and recent reduction in the devil population through DFTD is likely to be affecting both the populations of prey species and populations of the alien mesopredator, the cat. There is a strong indication that the native predators favour a more intact natural habitat leading to the possibility that managing the land to retain more native vegetation will benefit the native predators over the introduced cat.

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Chapter 1 General Introduction

1.1 Native versus invasive predator

Globally human activities including land clearing, habitat conversion and degradation, and human induced climate change are putting immense pressures on biodiversity. Current estimates suggest that 25% of mammal species, 13% of bird species and another 21,000 other species of plants and animals are at risk of extinction (Tilman et al., 2017, Johnson et al., 2017, Maxwell et al., 2016). Habitat change is a primary cause of species decline and extinction (Newbold et al., 2015), but in many places invasive predators, often favoured by habitat change, also have large impacts on biodiversity (Doherty et al., 2016b).

These alien predators affect both prey and native predator guilds, predominantly through direct predation, competition between the invader and native predators and disease transmission. Their adaptability both in habitat preferences and prey choice, assists in their establishment and is often facilitated by human interference through direct introductions into a perturbed landscape, allowing the invasive species to establish with little competition (Farris et al., 2017, Macdonald, 2016). The threats from invasive predators are magnified where native prey are vulnerable to them due to a lack of appropriate responses to the new threat (Doherty et al., 2015, Doherty et al., 2016b). The rate of extinctions in Australia through naïve responses by the critical weight range native species to predation by foxes and cats, suggests that Australian native fauna have been particularly strongly affected by invasive predators (Woinarski et al., 2015).

In contrast, in undisturbed natural landscapes, sympatric native predators can coexist with their prey species through evolved behaviours and morphologies that advantage the prey species through appropriate and rapid responses, giving them a greater chance of escape (Salo et al., 2007, Doherty et al., 2016b).

1.2 The ecological significance of top predators

Coexistence of sympatric apex or top predators in a natural system and mesopredators (lower order predator species) usually results from some form of segregation of habitat use; temporal, spatial or dietary, to minimise competition between species (Fedriani et al., 1999, Jones and Barmuta, 1998, Jones and Barmuta, 2000, Chen et al., 2009). When the niche they occupy is similar there can be direct competition for food resources and denning sites (Glen and Dickman, 2006b). However the loss of any mammalian predator species or introduction of new species, particularly when there is

also widespread disturbance to their habitat, can cause complex and unexpected interactions within the ecosystems (Milstein and Goldsmid, 1997, Glen and Dickman, 2005a). Generalist mesopredators freed from the controlling influence of an apex predator in new and often anthropologically perturbed environments, can give rise to trophic cascades leading to a loss of prey species, changes in communities and local extinctions (Prugh et al., 2009).

An intact predatory guild, including the top predators, exerts top down control on populations of smaller predators through competition for resources, intraguild predation and interference competition (Brook et al., 2012, Steinmetz et al., 2013). Declines in top predators can lead to release of middle order predators from their usual population controls, a process termed "mesopredator release". Where an apex carnivore is missing there can also be loss of regulation of larger herbivore populations leading to unhindered population increase with resulting impacts on vegetation communities (Elmhagen et al., 2010, Ritchie and Johnson, 2009, Dickman et al., 2014). Significant changes to the structure of fauna communities, as well as vegetation and even land forms can follow. Thus, top order predators play a role in regulating ecosystems (Ritchie and Johnson, 2009, Estes et al., 2011). Maintaining or restoring top predators in their natural habitat can provide greater resilience in natural systems, enhancing conservation of biodiversity (Elmhagen et al., 2010, Krofel et al., 2017).

Throughout the world, apex predators are facing population declines, and in many instances, extinction in the wild (Ripple et al., 2014). The causes are typically a combination of persecution by humans, loss and fragmentation of habitat, depletion of prey species, and spread of invasive species and disease (Wilcove et al., 1998, Wang and Macdonald, 2009, Prugh et al., 2009, Karanth et al., 2011, Newbold et al., 2015). However, maintaining populations of larger carnivores, particularly 'hypercarnivores' which depend almost exclusively on the flesh of vertebrates, requires large areas as they are typically found at low densities (Crooks, 2002, Glen and Dickman, 2006b).

A positive example of a successful reintroduction of a top predator assisting in ecosystem recovery is the grey wolf in Yellowstone National Park. Following loss of the wolf *Canis lupus* from the Park 70 years ago, abundance of elk *Cervus elaphus* increased to the extent that they suppressed recruitment of woody plants, in turn reducing habitat for other species (Ripple and Beschta, 2003). Fifteen years after reintroduction of wolves, elk have been pushed back to the hills so that elk numbers have declined in the valley bottoms, woody species such as aspen *Populus tremuloides* and cottonwood *Populus spp.* are re-establishing, populations of beaver *Caster canadensis* and bison *Bison bison* are recovering and bird species not seen for many years are returning (Ripple and Beschta, 2012).

1.3 Mammalian predators in Australia

Broad scale land clearance for agriculture in Australia over the last 200 years, along with introduction of invasive species, habitat fragmentation, altered fire regimes and harvesting of species, have resulted in the extinction of 26 mammal species (>10% of Australia's 273 terrestrial species), equating to 30% of the world's mammal extinctions over the last century (Morton et al., 2014, Woinarski et al., 2015). The predator communities of mainland Australia in particular have undergone significant alteration. The dingo *Canis lupus dingo*, believed to have arrived with early Asian seafarers 3500 to 4000 years ago (Gollan, 1984) with mitochondrial DNA indicating links of Asian origin at ~5000yr BP (Savolainen et al., 2004, Oskarsson et al., 2012), is implicated in the extinction on the mainland of the thylacine *Thylacinus cynocephalus* and the Tasmanian devil *Sarcophilus harrisii* (Glen et al., 2007) although there are other probable factors that may have contributed (Johnson and Wroe, 2003, Prowse et al., 2013). This has resulted in the dingo and more recently domestic dog hybrids with the dingo, becoming the apex carnivore over much of mainland Australia.

European settlers introduced other smaller predators including the red fox *Vulpes vulpes* and cat *Felis catus*, as well as a range of herbivore species with major impacts on the native prey species within the critical weight range of 350 – 5000g (Short and Smith, 1994, Read et al., 2001). Native predators and ecosystem resilience may have played a part in hindering the introduction of the European rabbit *Oryctolagus cuniculus* to Australia (Peacock and Abbott, 2013). Prior to 1900 before extensive loss and fragmentation of habitat, and establishment of populations of competing invasive mesocarnivores (foxes and cats), quolls and other native predators were credited with unsuccessful early attempts to introduce rabbits to Australia. It was only after sustained persecution on the predator guild (by hunting and broad-scale poisoning, including strychnine, but also cyanide and phosphorus) and increasing land-clearing that rabbit populations began to expand. The rabbit is now established across 60% of Australia and has caused major degradation of the Australian environment. Rabbits displace native browsers and compete for burrows and food, reduce regeneration of native vegetation and indirectly alter vegetation communities, and their numbers in turn support the invasive alien predators, foxes and cats.

These alien predator species are largely responsible for the extinction and population decline of many critical weight range native species including the loss of up to two thirds of burrowing mammals on mainland Australia (Doherty et al., 2016b, May and Norton, 1996, Read et al., 2001, Moseby et al., 2005). Present-day interactions between the fox, cat, rabbit and native fauna on

mainland Australia indicate the dingo is likely to be acting as an apex predator with some controlling influence on the introduced mesopredators, the red fox and cat (Glen et al., 2007, Letnic et al., 2012). Fox and cat populations likewise influence each other. It was found the cat population at one site on mainland Australia where foxes had been reduced, was three times higher than the corresponding non-treatment site, indicating a "release" of the cat population when fox numbers were reduced (Reddiex et al., 2006). The invasive predators similarly have an impact on the only remaining medium sized marsupial carnivore on mainland Australia, the spotted-tailed quoll *Dasyurus maculatus.* There is niche overlap and intraguild competition and/or predation between the introduced eutherian predators and the quoll (Glen and Dickman, 2008).

Whilst Tasmania retains much of its native forest cover, there has been extensive clearance, modification and fragmentation of this forest cover for agriculture, urban development and forestry since colonisation by Europeans. This is having a continued impact on the native biodiversity of this island state. One hundred years ago, Tasmania still had the last fully intact guild of marsupial carnivores in the world, the largest of these being the thylacine *Thylacinus cynocephalus*, the Tasmanian devil *Sarcophilus harrisii,* the spotted-tailed quoll *Dasyurus maculatus maculatus* and the eastern quoll *Dasyurus viverrinus*. The last known living thylacine died in captivity during the 1930s and the species was declared extinct in 1986 (Department of Sustainability Environment Water Population and Communities, 2013b), as the result of persecution and (possibly) disease.

As the dingo was never introduced to Tasmania, the devil assumed the role of top predator following the extinction of the thylacine. Tasmania's community of marsupial predators remained stable, albeit without the thylacine, for another 100 years until the emergence in the mid-1990s of a novel transmissible cancer, Devil Facial Tumour Disease (DFTD). Since it was first detected in 1996, this disease has caused an overall 84% population decline in the devil, with local declines in excess of 90% in long-diseased areas and the species is now listed as endangered (McCallum et al., 2007, Hollings et al., 2013a, Jones et al., 2008) although recent evidence suggests some limited recovery possibly due to co-evolution of devils and the disease.

The next largest member within the Tasmanian marsupial predator guild, the spotted-tailed quoll, which is also listed as threatened, may be sufficiently genetically distinct from the mainland populations to warrant subspecies classification (Department of Sustainability Environment Water Population and Communities, 2013a, Firestone et al., 1999). As with the devil, this quoll is almost exclusively dependent on vertebrate prey, and individuals require large areas to supply their prey requirements (Crooks, 2002). Although it is opportunistic and versatile, its prey is primarily medium sized mammals, defined variously as 500 g to 5 kg (Belcher, 1995, Belcher et al., 2007, Jones and

Barmuta, 1998), or 500g to 7 kg (Glen and Dickman, 2006a, Glen and Dickman, 2008). I use 500g to 7 kg to ensure the pademelon is included in this category, as it is known to be a prey species of the quoll, devil and cat (Fancourt, 2015, Jones and Barmuta, 1998, Glen and Dickman, 2005). There remains high mortality from human persecution, because some of its food is supplied by raids on chicken coops, and deaths from road collisions when scavenging road kill (Department of Sustainability Environment Water Population and Communities, 2013a) (Belcher et al., 2007).

The eastern quoll *Dasyurus viverrinus* is a smaller member of the marsupial predator guild. A large proportion of its diet is made up of invertebrates but it will also opportunistically take small mammals. Its population until recently was considered stable, however there have been recent reports of declines, possibly as a result of climate fluctuations and increased predation by cats (Fancourt et al., 2013, Hollings et al., 2013b). The eastern quoll is most abundant in the more open and drier woodland and grasslands country of eastern Tasmania and the highlands (Fancourt et al., 2013). The smaller extant marsupial carnivores include the dusky antechinus *swainsonii,* swamp antechinus *Antechinus minimus,* Tasman Peninsula dusky antechinus *Antechinus vandycki* sp. *nov*. and white-footed dunnart *Sminthopsis leucopus.*

Foxes have not established a population in Tasmania despite several illegal releases over the last 100 years and a more recent attempt between 1998 and 2001 (Sarre et al., 2013). However, cats were introduced at the time of European settlement (Abbott, 2002) and have become established in all habitats in Tasmania. Initially the perception was that the cats were having little impact on the abundance and diversity of native fauna in Tasmania (Abbott, 2002). However, in recent years, evidence is emerging that cat numbers are increasing, coinciding with the severe decline of the devil population over much of the State. There were indications the devil, as the current apex predator in Tasmania, was influencing the overall population of cats and that the decline of the devil population in recent years has resulted in mesopredator release within cat populations (Hollings et al., 2013b).

The devil may have played a role in suppressing the population of cats and is known to compete for resources with spotted-tailed quolls and eastern quolls, with a dietary overlap observed between these sympatric carnivorous marsupial species (Jones and Barmuta, 2000). This suppression effect is implicated in apparent avoidance behaviour by cats where devils are present (Lazenby and Dickman, 2013). Mesopredator release associated with the decrease in population of the devil is likely to impact on the dynamics of the lower order predatory species, including cats (Hollings et al., 2013b). While the decrease in devil population may have led to an increase in numbers of cats, the effects on quoll populations of the combined loss of devils and increase of the cats is unknown.

1.4 Effects of landscape modification for forestry and agriculture on Tasmania's native predators

Human land use has resulted in extensive changes to the landscape of Tasmania. While disturbance to natural systems is generally seen as detrimental to biodiversity, there are examples where managed landscapes can benefit species. For example, managed grazing and fire can maintain species in native grassland that might otherwise disappear (Kirkpatrick et al., 2005). However, the extent and composition of forest communities in Tasmania since European settlement (Michaels et al., 2010) has been markedly altered through continued extensive habitat loss, fragmentation and conversion of forest to agriculture and plantation forestry. This could have significant impacts on the biodiversity of the region.

While eucalypt plantations, particularly monocultures, are generally considered to have little biodiversity value in comparison to native vegetation communities (Kanowski et al., 2005)., some may still contribute to the maintenance of local biodiversity. The stream-side reserves and other areas of native vegetation retained for non-wood values (e.g., threatened species, visual landscape values, cultural heritage) during the establishment of a plantation (Forest Practices Authority 2015) may all contribute to the persistence of species. Some of the negative effects of plantations, however, include an increase in weed and feral pest species, potential for the introduced plantation tree species to invade adjacent native forest, potential for escape of genes into the native forest through hybridisation and loss of faunal habitat features found in native forest communities (e.g. tree hollows, dense understorey) (Lindenmayer and Hobbs, 2004).

Fauna using these monoculture plantations are more likely to be pioneer or generalist species and so represent only a fraction of the species typically found in native forest. A notable reason for the decrease in species diversity is loss of structural complexity within plantation stands, both eucalypt and conifer (Catling and Burt, 1995, Lindenmayer and Hobbs, 2004, Kanowski et al., 2005). For instance, one important adverse impact of structural simplification within plantations is the loss of hollow dependent species, that are virtually absent in plantations where there are few native forest remnants or surrounding mature native forest (Lindenmayer and Hobbs, 2004).

There are many examples of species dependence on this structural diversity. In plantations where windrows, woody debris and mounding are present, populations of invertebrates can be found similar to the adjacent native vegetation (Bonham et al., 2002, Grimbacher et al., 2007). The abundance and number of species of small and medium-sized mammals in eucalypt forests in south-

eastern NSW is influenced by the complexity of the understorey (Catling and Burt, 1995). Structural elements and habitat connectivity were found to influence the species richness and diversity of insectivorous bats and hollow dependent arboreal mammals in European farmland and eastern Australia respectively (Frey-Ehrenbold et al., 2013, Goldingay et al., 2015). Habitat suitability for martens in native forest and plantations in the USA and UK was found to be related to the availability of structural elements (Hearn et al., 2010, Caryl et al., 2012). Older plantations with more structural elements were found to provide habitat for a richer array of bird species in northern NSW (Hsu et al., 2010)

This indicates plantations managed for increased structural complexity, can result in restoration of ecological processes and a more diverse biota (Hartley, 2002, Lindenmayer and Hobbs, 2004). Retention of native vegetation remnants and providing structural elements such as diversity in plant form and species, windrowing, mound ploughing, and provision of large woody debris through pruning and thinning, have all been shown to provide habitat for different faunal groups and is essential to improving the diversity of biota within plantations (Munks and McArthur, 2000). With large areas of plantation across Australia, there is likely to be increasing community demand to manage plantations for biodiversity and to retain key environmental processes. In addition, the world markets for plantation products will require the maintenance of ecological standards for the certification of plantations (Lindenmayer and Hobbs, 2004).

The effects of plantation expansion on the marsupial carnivores have not been widely studied, but there have been conflicting results from studies on spotted-tailed quolls (mainland Australia and Tasmania) and devils (Tasmania). Spotted-tailed quolls prefer forests with structural complexity, including intact canopy and diverse understorey of shrubs, ground cover and woody debris (Belcher and Darrant, 2006, Troy, 2014). Although they will use vegetation patches within agricultural land primarily as corridors for dispersal, these areas do not appear to meet their resource demands (Troy, 2014). However, in contrast Saunders (2012) found devils, quolls and cats to have higher occupancy rates in fragmented rather than intact vegetation in a coastal landscape in northwest Tasmania. This area corresponded to highly productive landscapes with elevated small, medium and large prey numbers. Neither of these Tasmanian studies looked at occupancy and use of plantations by quolls or devils, or factors influencing breeding in this disturbed landscape.

1.5 Study Aims

The major aims of this project are to determine how the devil, quoll and invasive feral cat, are interacting in and using, a highly disturbed landscape. I will do this by surveying a disturbance gradient from native forest (both relatively intact and regenerating after harvest), plantation forests (including remnant patches of native forest and riparian reserves within plantation), through to the fragmented forest patches in and around agricultural land. Identification and understanding of habitat requirements of and relationships between native marsupial carnivores and an invasive eutherian carnivore within a highly modified landscape, including plantations, may inform land management decisions for the benefit of the marsupial predator guild.

This study aims to determine how devils *Sarcophilus harrisii*, quolls *Dasyurus maculatus maculatus* and cats *Felis catus* use this modified landscape in NW Tasmania and the relationships between the three species. By identifying key structural features within the landuse types we may have the opportunity to enhance land management practices to benefit the native marsupial predators over the cat. Key questions are:

1. What are the landscape factors influencing why some modified landscapes provide more suitable habitat than others for devils and quolls?
2. Can we identify the structural components at a site level, with particular reference to plantations, preferred by native predators?
3. How do devils and quolls use the landscape with the respect to each other and cats, and do any of the three predator spp. influence the way the landscape is used by the other two species?

The study was designed to look at site and landscape factors across a large study area to determine why some areas provide more suitable habitat than others for devils and quolls. Comparison of presence/absence and abundance data of each species across the major habitat types against the measured variables at both site and landscape level allows us to determine whether the species are indeed using the landscape differently, and the major factors associated with this difference. These measurements were also designed to determine the features of the landscape and ecosystems that attract cats.

Chapter 2 : Response of native and invasive predators to site and landscape-level factors

2.1 Introduction

Humans are now recognised as the primary cause of extinction of wildlife worldwide, with extinctions occurring at 1000 times the likely background rate (Pimm et al., 2014) and large carnivores are particularly at risk due to persecution, loss of habitat and loss of prey species (Macdonald, 2016, Woodroffe, 2000, Newbold et al., 2015). Despite a comparatively small human population, Australia has experienced the highest rate of mammal extinctions globally, with 22% of mammals and including more than 10% of endemic land mammals disappearing in the 200 years since European colonization (Woinarski et al., 2015). Human induced habitat change remains a factor in the decline and extinction of these mammals. For example, management of pastures and rangelands for livestock and simplification of vegetation structure as a result of changed fire regimes have reduced habitat quality for many species (Banks and Dickman, 2007). Another major cause of loss of native mammal species is the introduction of alien species, in particular the cat *Felis catus* and red fox *Vulpes vulpes* (Woinarski et al., 2015, Dickman et al., 2014), which prey on native species that may be naïve to them (Banks and Dickman, 2007, Salo et al., 2007). These two factors can act in combination. For example, Glen and Dickman (2011) found spotted-tailed quolls *Dasyurus maculatus* were more abundant in forests with more structural complexity and larger intact forest area, where there is likely to be lower abundance of foxes.

The island State of Tasmania has a higher proportion of its original cover than other parts of Australia, with significant areas of forests, woodlands and grasslands remaining unaltered. Land clearing for agriculture in Tasmania has occurred particularly in the fertile country at lower altitude, while forestry activities (native forest and plantation management) generally occur at higher elevations. Forestry and agricultural activities, combined with urban development have resulted in reduction of the original forest cover of c1750 to approximately 25% of old growth forest cover in the two hundred years post European colonization (Forest Practices Authority, 2012b).

Loss of habitat through clearing and conversion of native forest, native grasslands and scrubland, inevitably results in the loss of biodiversity (Fahrig, 2003). Changes to habitat affect fauna differentially. In Tasmania, some mammal species such as the Tasmanian pademelon *Thylogale billardierii* appear to benefit from forest fragmentation and the introduction of exotic pasture species in proximity to refuge (Norton et al., 2010), while other species are likely to experience population decline through loss of habitat. As in mainland Australia, changes to habitat in Tasmania have facilitated the increase in populations of alien species, including rabbits *Oryctolagus cuniculus*, black rats *Rattus rattus*, fallow deer *Dama dama* and the cat *Felis catus.* Invasive herbivores cause further changes to vegetation and thereby degrade the habitats of native species, while predation by

cats has direct effects on some prey species. Cats may also spread diseases such as toxoplasmosis to some native species (Bryant and Jackson, 1999, Fancourt et al., 2013, Hollings et al., 2013b). The combined effects have seen large declines in some species. For example, the eastern barred bandicoot *Perameles gunnii,* which is endangered on mainland Australia, has declined throughout the Tasmanian Midlands, persisting only in isolated populations where shrubs and ground cover remain to provide refuge from cats (Bryant and Jackson, 1999). This species is particularly vulnerable to infection by *Toxoplasma gondii* carried by cats and infected animals typically die within 2-3 weeks of infection (Bettiol et al., 2000).

In addition to effects of habitat change and invasive species, the native predator community of Tasmania has changed in ways that could have important effects on the ecology and abundance of surviving species. The loss of Tasmania's apex predator, the thylacine *Thylacinus cynocephalus),* which is believed to have gone extinct in the 1930s, may have allowed increase in the population of the second largest predator, the devil *Sarcophilus harrisii* through mesopredator release during the remaining decades of the 1900s. The emergence and spread across most of Tasmania of a novel lethal transmissible cancer, devil facial tumour disease (DFTD), first detected in 1996, has since caused declines of up to 85% of the total population of devils *Sarcophilus harrisii* (Hendricks et al., 2017), (McCallum et al., 2007, Jones et al., 2008). Persecution of the devil and quoll *Dasyurus maculatus maculatus*, a cat-sized marsupial predator, still occurs due to their propensity for attacking and killing domestic chickens. The cat became established throughout Tasmania following introduction at the time of European settlement (Abbott, 2002) and competes to some extent with the native predators in addition to carrying the disease, *Toxoplasmosis gondii* (Hollings et al., 2013b).

The quoll occurs in a wide range of habitats but is most common in wet forests, both rainforest and closed eucalypt forest (Jones et al., 2001, Glen and Dickman, 2011). The devil is also predominantly a forest-dweller, favouring sclerophyll forest and coastal scrub (Guiler, 1970). These habitats provide both species with forest-dwelling prey and large trees that furnish den-sites. Fragmentation can lead to an increase in the population of some prey species. Availability of exotic pastures adjacent to forest remnants providing shelter during the day, results in large populations of herbivores (Norton et al., 2010). The most widespread of the herbivore species are the medium-sized prey species Tasmanian pademelon *Thylogale billardierii*, brushtail possum *Trichosurus vulpecula* and the introduced rabbit *Oryctolagus cuniculus.* The larger Bennett's wallaby *Macropus rufogriseus* and wombat *Vombatus ursinus* are also common in some areas (Norton et al., 2010). Increased populations of potential prey at the interface between bush and pasture can provide prime hunting for predators (Duffy et al., 2007, Saunders, 2012).

We have little information on the effects of forest fragmentation on the distribution and abundance of native and alien mammalian predators in Tasmania (May and Norton, 1996, Banks et al., 2005, Gerber et al., 2012). Troy (2014) found quolls were restricted to patches of forest and scrub in a predominantly agricultural landscape in northwest Tasmania. Saunders (2012) found occupancy by quolls, devils and cats was affected by fragmentation, resulting in higher populations in a fragmented rather than in an intact landscape. Andersen (2016) used GPS tracking to show spotted-tail quolls and devils selected linear features such as roads, fence-lines and forest/ agricultural land edges, suggesting these features of fragmented landscapes can improve habitat quality for these species. However, home ranges were larger and distances travelled each night were greater in fragmented landscapes, suggesting resource density may have been lower (Andersen, 2016, Troy, 2014). As yet, no study has examined how availability of prey, landscape structure use and site-level features interact to determine site use by devils, quolls and cats.

There are many examples where intraspecific competition occurs between predator species. This may take the form of direct persecution, including hunting and killing of the smaller predators by apex predators (Sweitzer and Furnas, 2016, Krofel et al., 2017), or avoidance behaviours to reduce direct competition including dietary, spatial or temporal separation (King et al., 1996, Glen et al., 2011).

Studies in Tasmania have found some degree of dietary overlap between the extant sympatric marsupial predators including the spotted-tailed quoll and devil (Jones and Barmuta, 1998, Andersen et al., 2016, Andersen et al., 2017) and with a similar body-size it could be expected there would be some dietary overlap between cats and the quolls in particular. Where devil populations have declined through the DFTD, spotted-tailed quolls have expanded their dietary range to include larger prey, suggesting some competitive release (Andersen et al., 2017). However, few studies have investigated the occupancy and abundance of quoll, devil and cat across the landscape to determine if these species may use avoidance strategies to avoid direct competition. There is a strong probability that interspecific competition could influence abundance and distribution.

This study aims to investigate the use of a large, complex and perturbed landscape by quolls, devils and cats in northwest Tasmania. These landscapes include selectively logged native forest, a small amount of native grasslands, agricultural land and plantations established on farmland or by conversion of native forest. The study area was internally heterogeneous which, containing strata modified to various degrees by conversion of the original habitat to agricultural land and plantation forest, allowed me to test influences on local abundance of both landscape-level and site-specific factors associated with each species. My hypothesis is that the native predators will occupy forests

and plantations with greater structural complexity, while cats may be more abundant in the simpler habitat adjacent to farmland. The questions are:

- What are the landscape and site-level factors that make some habitats more suitable than others for devils and quolls?
- How do devils and quolls use the landscape with respect to each other and cats, and is there any indication of any predator species influencing habitat use by the other two species?

2.2 Methods

2.2.1 Study Area

The study area was a landscape of approximately 250,000 ha (32 km by 80 km) in north-west Tasmania, Australia (Figure 2-1). It was bounded in the north east by Harford, a farming region at an elevation of 6 m above sea-level (River Forth) with average annual rainfall 898 mm (East Sassafras) and annual mean maximum temperature (Devonport Airport) of 16.9^{O}C. The south west boundary was the small hamlet of Waratah, 42 km inland, with an elevation of 675 m, average annual rainfall of 2,180 mm and annual mean maximum temperature of 12.3 ^{O}C (Bureau of Meteorology).

The area comprises a complex mosaic of farmland, forested land (native forest and plantations) and native forest fragments within both the farmland and the plantations, intersected by numerous streams and rivers (Figure 2-1). The fertile coastal lowlands have been mostly converted to agriculture although patches of native vegetation are retained on steep slopes and areas not suitable for cultivation. Predominant land uses are cropping and grazing on the rich ferrosol soils in the north-east, and plantation and native forestry in the south and west. The farms are often mixed enterprises with dairy farming in conjunction with growing a range of medicinal and food crops such as poppies, pyrethrum, potatoes, onions, legumes and brassicas. Further inland and to the south, the country becomes steeper and colder with increasing elevation and is less suited to intensive agriculture, and is replaced by more extensive grazing and forestry. Conversion of native forests to plantations on public land ceased in 2006, during the period between 1996 and 2011 when rapid expansion of plantation forestry was occurring in the region (Forest Practices Authority, 2012b).

A pilot study was conducted in the Upper Natone area in December 2013 and January 2014. Twenty cameras were set for 21 days within a 90 km^2 area in two habitat types, native forest and agricultural margins. The pilot study established the presence of the three predator species in both vegetation/land use types and recorded a few cases of facial tumour disease in devils.

A set of 300 potential sites, distributed across each of the four vegetation/land use types, was randomly generated using GIS (ArcGIS 9.3). To ensure the sites were accessible in all weathers, potential sites were located within a 500m buffer placed around all the roads and tracks in the study area. Sites were assigned a unique number in the nested design, with equal numbers of replicate camera sites (n = 90) in the three major vegetation and land use types — native forest, plantation and agricultural land — and 30 in native grassland/moorlands, of more limited extent within the study area. From these, 150 sites were selected for the survey, allowing for attrition in site selection at both GIS and field stages. Potential sites were checked visually in map view. Sites close to the

edges of adjoining vegetation and land use types were discarded, and in cases where two sites were within 1 km of another, one was discarded to maintain at least 1 km separation of survey sites. The remaining sites were randomly divided into three groups to be surveyed in three consecutive rounds of deployments of 50 cameras each. Sites for each deployment were spread across the geographic extent of the study area and maintained the ratio of vegetation/land use types. All sites were visited in March 2014 to check accessibility and nominal vegetation type, before the first survey in May 2014. Camera sites were established within 200m of the computer-generated point or discarded, for example if topography proved unsuitable, vehicular access was restricted (for example, by fallen trees over the track) or if vegetation cover had changed since the most recent GIS map layer. Potential sites on the list were visited until the required number of sites for each grouping was reached, as follows: 44 sites on the edges of agricultural land (abbreviated as AG), 45 on plantation (PL), and 46 on native forest (NF) with 15 sites in native grasslands/moorlands edges (GL) (Figure 2-1). Within each of the major vegetation / land use types, approximately equal numbers of sites were placed in areas either with or without major structural elements, including windrows of dead fallen timber remaining from logging activity, individual logs, and large rocks.

Two surveys were conducted—in autumn/winter (May to August 2014, henceforth "winter") and spring/summer (November to February 2014-2015, henceforth "summer")—to capture seasonal variation in detection probability, occupancy or abundance of wildlife.

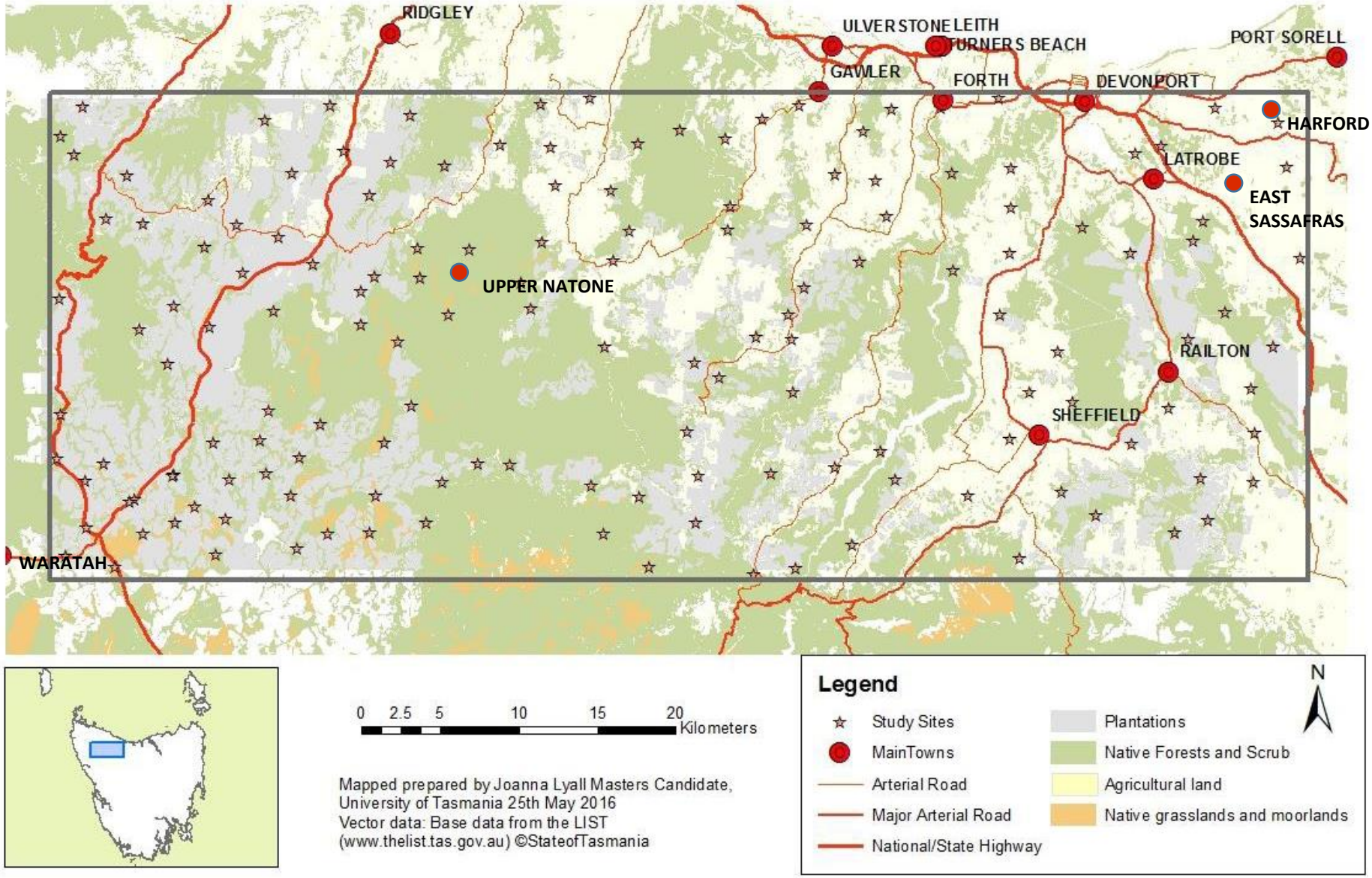

Figure 2-1 Map showing study area with the position within Tasmania indicated in the inset map (Southwestern-most point latitude -41.443865, longitude 145.582512 and northeastern-most point latitude -41.203092, longitude 146.508051)

2.2.2 Camera deployments

Fifty Reconyx HyperFire PC800 cameras were deployed in three rounds to complete the 150 sites in each season, a season being defined as a maximum four-month period. Cameras were set for between 21 and 30 days to give a standardised minimum period of 21 days from when the camera was set, following Robley et al. (2010). The cameras were not revisited during that time. This period was considered sufficient to provide a reasonable chance of detecting cryptic species such as quolls and cats. The 50 individual cameras were not deployed in the same locations across winter and summer rounds but records of their performance allowed individual cameras to be traced. The mean distance between camera sites was 2680 m (median 2640m) with a maximum of 5833 m and minimum of 1232 m.

At a local scale, the cameras were placed to maximise the chance of detecting a predator. Cameras were placed adjacent to animal pads, tracks or roads or where there was obvious sign of predator and prey activity, but out of direct sight of regularly used access roads. The cameras were firmly attached to a suitably positioned tree, or to a stake if there was no available tree, using octopus-straps, at approximately 1.5m above ground level depending on site conditions such as vegetation and slope. A bait canister containing attractant bait, and a visual lure were suspended 1.5 m from the camera at a height of 1.5m above ground. Each camera was set so the field of view focused downward on the area below the bait canister and lure, using a wedge or piece of wood positioned between the top of the camera and the tree or stake to adjust orientation. Positioning the lures above the ground both protected them from interference by passing animals and encouraged animals to stretch up, in some cases allowing identification of sex, maturity and, individual animals by unique coat markings (Hohnen et al., 2012). Leaves or branches that wind might move were removed from the field of view of the camera to minimise false triggers.

Two types of lures were deployed at each camera. To attract visual predators, specifically cats (Reed, 2011, Bengsen et al., 2011), a visual lure in the form of a CD tied to a string so it could swing and rotate, was suspended beside the bait lure. A food lure consisting of a mixture of sardines and tuna oil to attract predators, and rolled oats and peanut butter to target herbivores (Hohnen et al., 2012), was used to maximise the chance of attracting and detecting a wide range of species (Reed, 2011). Increasing the efficiency of image capture by use of a baited lure allows more accuracy in identifying individuals, facilitating more robust capture–recapture analysis (Garrote et al., 2012). Three slightly different bait recipes were used over the winter survey due to variable supply of tuna oil. The bait recipe was recorded for each camera deployment. Bait 1 was the standard recipe detailed above; Bait 2 had no tuna oil but double the quantity of sardines, rolled oats and peanut butter; Bait 3 had a

different tuna oil containing blood, as well as the sardines, rolled oats and peanut butter. For the summer survey, all baits were of Bait 1 recipe. In the data analysis, the different bait recipes were tested for any effect on the detection of the target species.

It is recognised that using paired cameras allows more reliable identification of individuals through allowing a better view of unique markings on both sides of individuals (Rovero et al., 2013), however by using the bait lure to attract and hold the target species' attention, there is a greater chance of seeing identifying markings, while at the same time obtaining a larger number of individuals across a much wider area (Rovero et al., 2013). Robley et al. (2010) found the detection probability in comparing paired Reconyx cameras with a single Reconyx camera at each site was only slightly higher ($p = 0.077$ and $p = 0.060$ respectively). The limitations of using one camera per site is the loss of data if a camera malfunctions or is stolen. In this study, there were no malfunctions but one camera was stolen during the summer round, however this would have had little effect on the overall results due to the large number of sites.

For each camera deployment the unique ID number for that camera was recorded, as well as the GPS waypoint position (Grid ref, GDA 55), the date and time the camera was set and retrieved and the operating status of the camera on retrieval. The cameras automatically recorded ambient temperature and moon phase. For the winter round, an oversight led to the cameras being set to four image capture settings. These included: 10 shots followed by a three second gap (7 cameras); 10shots/1sec gap (6 cameras); 5shots/1sec (28 cameras) and; "Rapidfire"(109 cameras), which is 3 shots/ < 1sec gap and repeated while movement continues to be detected (Table 2-8, Appendix). The Reconyx PC800 has a trigger speed of 0.2 seconds (camera specifications) which maximises the chance of capturing any movement within the field of view (Meek et al., 2012), hence this difference in settings was considered to potentially affect the number of images captured for each visit, but not the likelihood of recording presence of species, or identifying individuals for estimation of abundance. This was checked as a detection factor during analysis. For the summer round all cameras were set to Rapidfire to ensure a maximum number of images of individual animals within the field of view.

Images were downloaded from the cameras as they were brought in, and batteries were recharged overnight so that the cameras were ready for redeployment. The images were processed using MapView Professional software, which allowed tick boxes to be set up for all species identified, as well as recording age, sex, start and end time of sequence, behaviour and any notes about the animal. However accurate identification of age and sex could not be assured and was not used. Dates and times of triggers were recorded. The best diagnostic image was selected from each sequence of images recorded during an encounter of an animal with the camera to represent the

entire sequence, with a start and end time for the sequence recorded. On this definitive image the species was noted along with the number of individuals present in the sequence and where possible age and sex were recorded. Sequences were noted from camera initiation to stop, whether the individual/s were visible or not, to capture length of time the animal was present around the camera site. For the three target species notes were taken to aid in identification of individuals on a nightly basis. Where Devil Facial Tumour Disease (DFTD) lesions were visible, this too was noted. The variables recorded from camera images are listed in Table 2-8 (Appendix).

2.2.3 Site-level environmental parameters

For each camera site, I recorded the camera number, elevation, aspect and slope of the site (See Table 2-8, Appendix). I recorded environmental parameters that could influence the presence and abundance of wildlife for each camera site (Table 2-9, Appendix). These included both site-level parameters recorded at the camera sites in the field and landscape-level variables measured from GIS layers. Site-level parameters were recorded following the winter survey and were re-measured only if they were likely to have changed between surveys. The variables were recorded at the time of camera retrieval to minimise disturbance to the site.

Structural elements that could influence movements, foraging or denning of predators and prey species were described. These included estimates of the height and percentage cover of the canopy, shrub layer, and groundcover (6 variables), and the percentage cover of rocks and logs >15cm diameter (2 variables) (Silvy, 2012) (Table 2-9, Appendix). Stem density was assessed by counting separately the number of stems greater than 10cm diameter at breast height (dbh) i.e. 1.3 m above ground, and the number > 2cm and < 10cm within a radius of 5m of the lure (2 variables). These are indicators of the density of undergrowth that could influence the way mammals travel through the area.

The amount of lateral visual obstruction caused by vegetation, rocks and logs was estimated using a variation of the "vegetation profile board" developed by Nudds (1977). A $1m^2$ white sheet, marked in a grid of 10 x 10 cm squares, was held by an assistant standing 5 m from the observer at the camera site and the percentage of the sheet visible was recorded. Visual obstruction was estimated at three different heights relevant to the visual scanning height of the different species of predators and prey; 25 cm above ground level for cats and quolls, 50 cm for devils and 100 cm for larger macropods, with the observer squatting to record the data at each height. This was repeated at the four cardinal points (north, east, south, west). The mean of the four measurements for each height was used in analyses (3 variables). No lateral visibility was scored as "0" while 100% visibility was scored "1.0".

Physical obstruction by vegetation in the vicinity of the camera site was measured using a 1m pole, marked at 0-10cm, 10-30cm, 30-50cm and 50-100cm, that was held vertically at 1m intervals between 2m and 5m from the lure, this being repeated in the four cardinal directions from the camera site. In each height category a "1" was recorded if vegetation touched the pole or "0" if there was no contact. The means of the scores for each distance and compass point from the camera at each height were used in analyses (4 variables). A cat, for example, moving through the landscape would encounter vegetation between ground level and approximately 30cm. A score of 0.75 for this height would indicate vegetation that physically obstructs the cat's movement in three of the four quadrants around the camera.

2.2.4 Landscape-level environmental parameters

Landscape-scale variables for each camera site, identified by a GPS location measured in the field (Garmin GPSMap76CSX GPS unit; GDA 1994 MGA Zone 55), were calculated in ArcGIS 10.1 from layers, including a vegetation community layer TasVeg 3.0, supplied under license to the University of Tasmania (Land Tasmania, 2015). I grouped vegetation communities into four broad vegetation types: native forest (including native scrub), native grassland (including moorland), plantation and agricultural land (Harris and Kitchener, 2005). To assess the degree of forest fragmentation and the proportion of major vegetation types in the vicinity of the site, I calculated the edge-to-area ratios and the proportions of each of the four major vegetation/land use types in three buffer sizes around each camera site, with 1km, 3km and 5km radii.

To assess structural complexity of forest vegetation, I recorded a mature habitat index using the index and GIS layer developed by the Tasmanian Forest Practices Authority (Koch et al., 2016, Forest Practices Authority, 2016), for each camera site. This index categorises mature eucalypt crown density and links the maturity of the canopy with the presence of structural complexity, including probable presence of hollows, large crowns and tree senescence by calculating the area of mature canopy at differing levels of density. Using the distribution of mature forest from satellite imagery, vegetation mapping data, previous forestry activities and fire, Koch et al. (2016) coded five categories of mature eucalypt crown density: -1 being land not naturally growing forest capable of forming a canopy; 0 with little canopy forming vegetation present; and 1-3 representing low, medium and high density canopy respectively. For analysis, I combined the codes -1 and 0 as these provide little or no canopy. I applied this mature forest index at the 1km and 3km radius buffers around each site.

To assess associations of the predator species with human structures in the landscape, distances to the nearest roads or tracks, drainage lines (river, stream), and buildings were calculated using ARC-GIS. Buildings mapped on GIS layers were classified as either residential (e.g. residence) or non-

residential (e.g. shed, public facility). These variables and codes used are shown in Table 2-9 (Appendix).

2.2.5 Night-level parameters

For each night-level factor that could influence the detection of the target species, a matrix was constructed indicating the state on each of the 21 nights at each site. Some factors were static for the survey period for each site (bait recipe, trapping session or round, land use) while others varied over the period (moon phase, sympatric predators, age of lure).

Parameters included in the analysis that could influence detection of the target species when present included:

- the camera trapping session (the round): first, second or third round of 50 cameras set in the winter or summer season, as within-season timing could influence detection;
- camera settings: confined to winter season, to check if the difference in camera settings influenced detection;
- bait mix: confined to winter season, to check if the difference in the bait mix influenced detection;
- age of the lure: loss of scent over time could influence the ability of the lure to attract predators;
- moon phase: the moon is recognised as a factor influencing the way some species move through the landscape (Daniels et al., 2001, Bethge et al., 2009);
- sympatric predators: number of other predators present on a nightly basis could influence the way a species will move around the landscape;
- land use: the vegetation/landscape use may influence whether the species can be detected.

2.2.6 Data handling and analysis

Images were downloaded with the camera metadata (date, time, ambient temperature) into a spreadsheet and each animal recorded on camera was identified to species. Images of the same species separated by 5 minutes or more were considered separate records. All three species of predators could be identified for each camera within each night using a combination of size and

natural markings; devils from their white markings, quolls from their unique spot patterns, and cats from colour and the unique patterns of stripes on their front legs (if present). I standardized descriptions of the markings to assist in matching detections of individual animals. For instance, there are three main areas on the body that may have markings for devils; the front of the chest, shoulders, and over rump in front of tail. The markings were described from the sequence of images as not all of the described markings were visible in the one definitive image. The left side (lhs) and right side (rhs) of the body is typically similar although dots and patches may be smaller or fainter on one side than the other. As an example, my descriptions for three devils (Figure 2-2 a-c) at one site over one night read:

a. "Stripe over chest broad in centre and extending down between front legs and across onto front of shoulders. Faint patch on lhs behind shoulder. Short stripe on rump"

b. "No visible markings from rhs"

c. "Stripe over lhs shoulder merging with crescent shaped patch behind shoulder. Broad stripe across rump. Rhs not visible"

Figure 2-2 Three devils identified at one site on one night showing the different markings used to determine that they were three unique individuals

Each site was checked and where there was more than one detection of a predator on any night, the descriptions and if necessary, the images were rechecked to identify if these detections were of one or more individuals. The number was amended if it was found to be a single individual returning on that night. If it was inconclusive, I marked the animal as a returning individual rather than a new individual. Table 2-1 indicates the reduction in total detections of quolls, devils and cats to individuals on a nightly basis for the two seasons.

Table 2-1 Number of individuals identified on a nightly basis for quolls, devils and cats, as used in the single species abundance model analysis for winter and summer seasons, with the total number of detections in parenthesis

	Winter nightly detections of individuals (Total detections in parenthesis)	Summer nightly detections of individuals (Total detections in parenthesis)
Spotted-tailed quoll	124 (147)	102 (124)
Tasmanian Devil	309 (349)	247 (267)
Cat	136 (197)	111 (134)

All other animals detected on the cameras were identified to species and the number of detections of each species each night on each camera was recorded to use as a predictor variable in the single species abundance models analyses for the three target species. These variables were included in the models to test the influence of prey species or the other predator species on the estimated abundance of the predator species or for prey species, a predictor variable influencing the abundance of a predator species. Species other than the three target predators were grouped as predator or prey species, by weight (species weights as per Strahan (1991) for mammals and "Birds in Backyards" webpage (Australia, 2016) for birds) and whether native or exotic. Numbers of detections are listed in Table 2-3 to Table 2-6 in the appendix. Various definitions are used for "critical weight range" native mammals, some with a top weight of 5000g, others to 7000g (May and Norton, 1996, Glen and Dickman, 2006a). I used 7000g to ensure the pademelon, a known prey species for the three target predators, is included in this grouping. For the "critical weight range" native prey grouping, (500g – 7000g) native species from Table 2-3 and Table 2-4 were grouped together. For the "sm_med_exotic" group, the exotic species from the same two tables were grouped together for analysis. Table 2-3 to Table 2-5 in the appendix list the potential prey species by size, season, vegetation/land use type, average weight for the species and status as native or exotic. Individual prey species included in the analysis were two native species, Tasmanian pademelons *Thylogale billardierii* and brushtail possums *Trichosurus vulpecula*, and the exotic rabbits *Oryctolagus cuniculus* and black rats *Rattus rattus.* Other prey species within the small and medium groups were detected at too few sites to produce meaningful results. However, all species were included in the size groupings for analysis.

Table 2-6 lists the predators detected by season and vegetation/land use type with their status as native or exotic and average weight for the species. Only the three target species were used for the

analysis as the other predator species were too rarely detected, being either single sightings or occurring at one or very few sites. Of the 57 species detected, 44 were native and 13 were exotic (including *Homo sapiens, Canis familiaris*, *Bos taurus* and *Ovis aries*) while several were unidentified. The identified species included 34 mammals, 22 birds and 1 reptile.

Data handling and analyses were conducted in R (Version 3.2), using the R-Studio (Version 0.99.896) interface and figures were created using the "ggplot2" package. A correlation matrix, using Pearson's r correlation, was constructed for all continuous site and landscape variables to reduce the variables for analysis. I used R version 3.2 using the R-Studio (Version 0.99.896) interface. Where pairs of variables were correlated with r >0.5, I selected one variable from the pair to use in the analysis. Scatter plots were inspected to further investigate the correlations. The variables retained to use in the modelling with their summary statistics are shown in Table 2-8 in the Appendix.

N-mixture models (Royle, 2004) allow an estimate of the total abundance of the target species at each site. I used N-mixture modelling with K=15 to estimate the direction and size of effect of the selected environmental parameters on the abundance of each predator species across the study area. Using temporal and spatial replication, which often produces sparse count data, N-mixture modelling allows estimates of a population size from surveys while accounting for imperfect detection (Royle, 2004). The site-specific population sizes are considered independent random variables however these can be influenced by the parameters chosen to estimate the abundance (Fiske and Chandler, 2011). Heterogeneity in the data may indicate there is some other covariate influencing the result of the modelling (Royle, 2004, Fiske and Chandler, 2011). As I was able to identify individual animals, I ran single species abundance models using the unmarked Point Count package "pcount" (Fiske and Chandler, 2015), for both the winter and summer "seasons". This provides an estimation of abundance of each of the predators at each site.

I constructed a set of plausible models representing hypotheses on the environmental factors influencing abundance of quolls, devils and cats in the landscape. These hypotheses were based on prior knowledge of the ecology of these predators (Glen and Dickman, 2006a, Jones and Barmuta, 1998, Andersen et al., 2016, Troy, 2014, Belcher and Darrant, 2004, Bengsen et al., 2012). The number of different parameters in each model was restricted to six for quolls and cats (detected at 68 and 66 camera sites, respectively, in the winter survey), and to seven for devils (detected at 74 sites), following the 10:1 rule of thumb for the number of cases to number of model parameters (Harrell et al., 1996). I modelled night level parameters affecting predator detection probability separately and incorporated the final set of night-level detection variables into the estimated abundance models. The detection factors tested are listed in *2.2.5 Night level parameters*, and

included the different bait recipes and settings (winter only), moon phase, lure age, the round in which the camera was set within the season, habitat and presence of the other predators. The adequacy of fit for the final model was checked with parametric bootstrapping. I used multi-model inference (Burnham and Anderson, 2002) with a nominal limit of ΔAIC <2 and model weights to rank the influence of different models in describing the abundance of predators. Only those parameters in the models that best fit the data and had a small standard error relative to parameter size (Z statistic >1) were considered to have a reasonable influence on the estimated abundance of the predators.

2.3 Results

Total sampling effort amounted to over 151,200 camera-hours, yielded 282,000 images and these were reduced to 230,000 images once false triggers were removed.

The distribution and abundance of the three target species was mapped for the study area in winter, when they were more active (Figure 2-5). The top panel illustrates that quolls were relatively evenly distributed across the study area; devils were more abundant at elevation and in larger contiguous areas of native vegetation in the south-western sector (indicated to the left of blue dotted line); while cats were more abundant within the agricultural areas in the north-eastern sector, but present in low numbers throughout the study area.

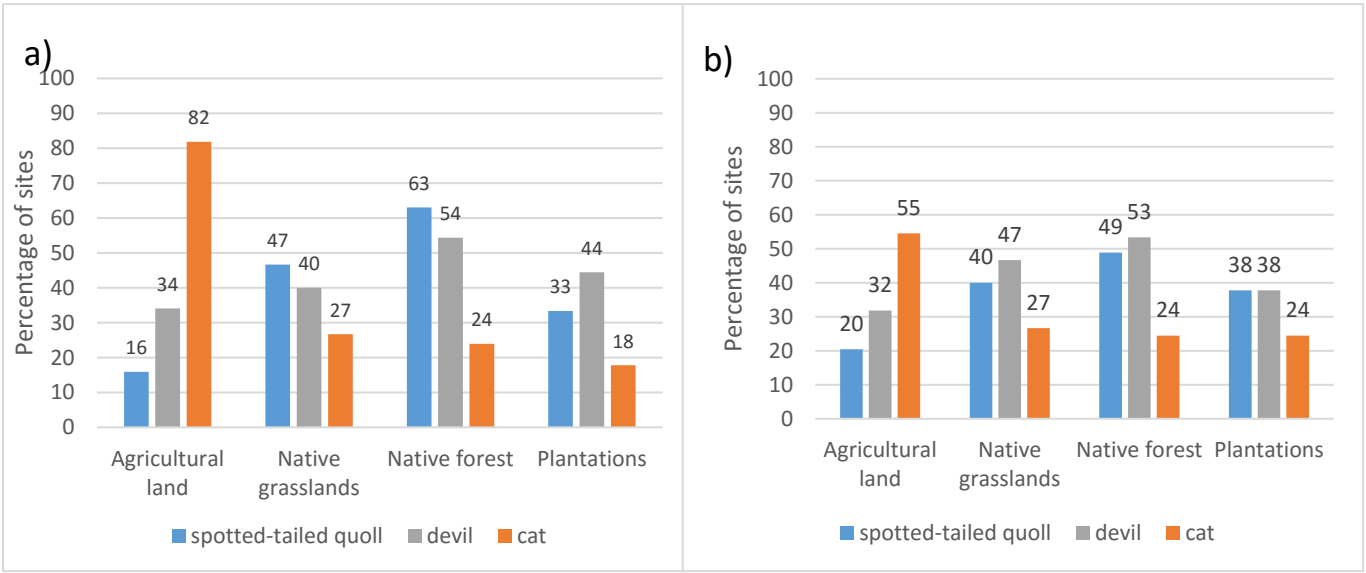

Figure 2-3 Percentage of sites with detections of spotted-tailed quolls, Tasmanian devils and cats within the four distinct vegetation/land use types in winter (a) and summer (b)

2.3.1 Potential prey species

Among the small (< 500g) animals detected (Table 2-3, Appendix), the black rat (Figure 2-6) was detected most often and was found in all vegetation and land use types, but was most consistently detected at agricultural sites. Black currawongs *Strepera fuliginosa*, blackbirds *Turdus merula* and Bassian thrushes *Zoothera lunulata* were detected regularly. Blackbirds were almost exclusively detected at agricultural sites, while black currawongs were found in agricultural and plantation sites in winter but across all vegetation and land-use types in summer. The Bassian thrush avoided native grasslands sites but was detected within the other three vegetation/land use types.

The most consistent detections from the medium weight animal group (>500g and 7000g) (Table 2-4) were the pademelon (Figure-2-8) and common brushtail possum (Figure-2-9). Very high detections of pademelons were found at some agricultural sites, however they were also detected frequently at a few plantation and native forest sites. Common brushtail possum detections were greatest at a few agricultural sites, particularly where there was an abundant food source to attract them. For instance, at AG75, the camera site was along a creek on a dairy farm. The maize-based silage pit two hundred metres away appeared a strong attractant to the local possum population and yielded more than 5000 images over the 21 days.

a). *Spotted tailed quoll - native predator*

b) *Tasmanian devil – native predator*

c)*. Cat - introduced predator*

Figure 2-4 The three target predators: spotted-tailed quoll (a), Tasmanian devil (b) and the introduced cat (c)

Rabbits were detected almost exclusively at agricultural sites (Figure 2-7). The southern brown bandicoot *Isoodon obesulus,* long-nosed potoroo *Potorous tridactylus* and eastern bettong *Bettongia gaimardi,* were frequently detected at a few sites across all vegetation and land use types. However, these native species were not present consistently enough to be included in the analysis on a species basis.

Among the large prey species (Table 2-5) wombats (Figure-2-10) were detected most frequently in native grasslands and moorlands, with plantations the next most frequent for detections. Native forest and agriculture had few sites with detections.

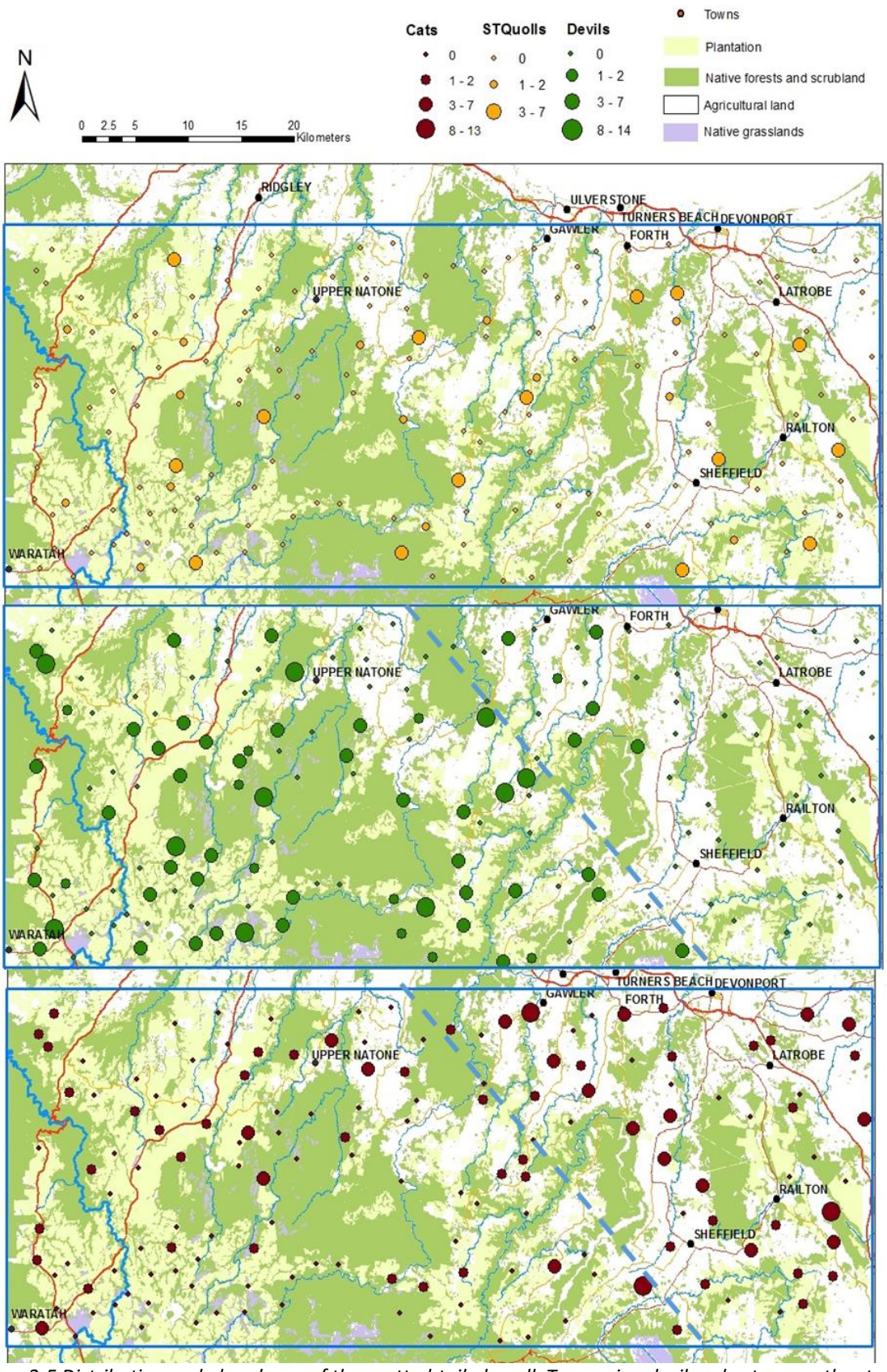

Figure 2-5 Distribution and abundance of the spotted-tailed quoll, Tasmanian devil and cat across the study area during the winter study season, respectively, in panels from top to bottom. Larger points equate to more detections at that site on a nightly basis. A blue dashed line demarcates an apparent division in the abundance of devils and cats, with devils more abundant to the west of the line and cats to the east.

Figure 2-6. Black rat - introduced prey species

Figure 2-7. European rabbit - introduced prey species

Figure-2-8. Pademelon - native prey species

Figure-2-9. Brushtail possum - native prey species

Figure-2-10. Wombat and young - native prey species

2.3.2 Abundance modelling of carnivore species

The estimated abundance models were run using the final set of night level parameters affecting predator detection. The candidate models were ranked to find the models that best described the estimated abundance of quolls, devils and cats. Table 2 2 indicates the best models including the factors found to influence detection, along with the site and landscape variables found to influence estimated abundance.

Table 2-2 .The final set of candidate models that describe the estimated abundance of spotted tailed quolls, Tasmanian devils and feral cats in a landscape in northwest Tasmania modified by plantation forestry and agriculture. Parameter estimates and their standard errors are provided for the influencing factors for predicted abundance; the abundance AIC value, delta AIC, AIC weight and cumulative weight and detection factors. For categorical parameter estimates, the different levels of the parameter are listed, with the category represented as the intercept in brackets. Moon phase:FQ = 1st quarter, LQ= Last quarter, NM= New moon, FM= Full moon; Bait mix: B1 = recipe 1, B2 = recipe 2, B3 = recipe 3; Round: SR1 = Summer round 1, SR2 = summer round 2, SR3 = summer round 3; Habitat: AG = Agricultural land, GL = Native grassland, NF = Native forest, PL = Plantation

Models								**Occupancy - abundance (ψ)**				**Detection (p)**		
Quoll														
Winter	**Intercept**	**Devil**	**Canopy height**	**CWR native spp**	**Stems <10cm**	**Cat**	**Nat. forest 1km**	**AIC**	**ΔAIC**	**AICwt**	**Cumtv/ Wt**	**Intercept**	**Lure age**	**Bait mix**
1	0.55 ± 0.35	0.27 ± 0.09	0.30 ± 0.11	0.25 ± 0.07	0.21 ± 0.09	-0.24 ± 0.16	0.02 ± 0.12	1010.64	0.00	0.95	0.95	-3.39 ± 0.40	-0.04 ± 0.01	(B2)-0.88 ± 0.57 (B3)-0.27 ± 0.24
	Intercept	**Devil**	**Sm/Med exotic spp**	**CWR native spp**	**Cat**			**AIC**	**ΔAIC**	**AICwt**	**Cumtv/ Wt**	**Intercept**	**Lure age**	**Bait mix**
2	0.41	0.32	0.10	0.23	-0.31			1016.76	6.12	0.05	1.00	-3.17	-0.04	(B2)-1.04± 0.58 (B3)-0.31 ± 0.25
Summer	**Intercept**	**Devil**	**Cat**	**Rat**	**Possum**	**Stem count >10cm**	**Shrub density**	**AIC**	**ΔAIC**	**AICwt**	**Cumtv/ Wt**	**Intercept**	**Lure age**	
1	-0.42 ± 0.27	0.9 ± 0.11	-0.36 ± 0.27	0.17 ± 0.08	-0.46 ± 0.27	0.34 ± 0.12	0.20 ± 0.13	836.08	0.00	0.71	0.71	-2.60 ± 0.30	-0.07 ± 0.02	

	Intercept	Devil	Rat	Possum	Stem count >10cm	Shrub density	Nat. forest 1km	AIC	ΔAIC	AICwt	Cumtv/ Wt	Intercept	Lure age	
2	-0.38 ± 0.26	0.14 ± 0.10	0.17 ± 0.08	-0.48 ± 0.29	0.32 ± 0.12	0.22 ± 0.13	0.08 ± 0.14	838.21	2.13	0.24	0.95	-2.6 ± 0.30	-0.07	
Devil														
Winter	**Intercept**	**(Log) elevation**	**Stquoll presence**	**Wombat**	**Nat. forest 1km**	**Stems <10cm**		**AIC**	**ΔAIC**	**AICwt**	**Cumtv/ Wt**	**Intercept**	**Lure age**	**Moon**
1	-0.16 ± 0.14	0.58 ± 0.15	0.24 ± 0.07	0.12 ± 0.07	0.26 ± 0.09	0.11 ± 0.07		1803.89	0.00	0.49	0.49	(FM) -1.80 ± 0.16	-0.02 ± 0.02	(FQ) -0.86 ± 0.34 (LQ) -0.16 ± 0.18 (NM) -0.79 ± 0.30
	Intercept	**(Log) elevation**	**Stquoll presence**	**Nat. forest 1km**				**AIC**	**ΔAIC**	**AICwt**	**Cumtv/ Wt**	**Intercept**	**Lure age**	**Moon phase**
2	-0.17 ±0.14	0.67 ± 0.14	0.24 ± 0.07					1804.43	0.55	0.37	0.86	(FM) -1.80 ±.16	-0.23 ± 0.02	(FQ) -0.85 ± 0.34 (LQ) -0.15 ± 0.18 (NM) -0.77 ± 0.30
Summer	**Intercept**	**(Log) elevation**	**Stquoll presence**	**Wombat**	**Nat. forest 1km**			**AIC**	**ΔAIC**	**AICwt**	**Cumtv/ Wt**	**Intercept**	**Lure age**	**Moon phase**	**Round**
1	-0.21 ± 0.14	0.23 ± 0.13	0.15 ± 0.07	0.28 ± 0.07	0.29 ± 0.10			1485.45	0.00	0.97	0.97	(FM) (SR1) -2.34 ± 0.24	-0.10 ± 0.03	(FQ) -0.76 ± 0.38 (LQ) 0.54 ± 0.26 (NM) 0.82 ± 0.48	(SR2) 0.90 ± 0.25 (SR2) 0.39 ± 0.27
Cat														
Winter	**Intercept**	**Ag land 1km**	**Rabbit**	**Landuse**	**(Log) elevation**	**CWR native**	**Stems <10cm**	**AIC**	**ΔAIC**	**AICwt**	**Cumtv/ Wt**	**Intercept**	**Lure age**	**Habitat**

							spp							
1	(AG) 0.48 ± 0.40	0.33 ± 0.22	0.12 ± 0.04	(GL) -1.70 ± 0.80 (NF) -1.70 ± 0.99 (PL) -0.71 ± 0.75	-0.13 ± 0.10	0.14 ± 0.06	0.27 ± 0.11	1134.83	0.00	0.97	0.97	(AG) -2.90 ± 0.29	-0.03 ± 0.01	(GL) 1.27 ± 0.5 (NF) -0.97 ± 0.97 (PL) -0.16 ± 0.59
Summer	**Intercept**	**Agland 1km**	**Stquoll presence**	**Devil presence**	**(Log) elevation**	**Small/med exotic**	**Canopy density**	**AIC**	**ΔAIC**	**AICwt**	**Cumtv/ Wt**	**Intercept**	**Habitat**	
1	-0.31 ± 0.27	0.05 ± 0.22	-0.30 ± 0.22	0.23 ± 0.11	-0.18 ± 0.16	0.08 ± 0.09	0.31 ± 0.13	857.10	0.00	0.82	0.82	-2.66 ± 0.25	(GL) 0.3 ± 0.63 (NF) -1.26 ± 0.48 (PL) -1.14 ± 0.49	

2.3.3 Spotted-tailed quoll abundance modelling

There was a single model in the final candidate set for quoll (Table 2-2 and Figure 2-11) in winter, with an AIC weight of 95%. The second model had a Δ AIC of 6.12, indicating the factors in the top model were the best fit for explaining the quoll abundance during winter. Quolls were detected where there were more devils, high canopy (older/taller trees), more critical-weight-range native prey and more stems under 10cm diameter. This would include native forest, plantation and vegetation at the edges of agricultural land as this model did not discriminate between land uses. Fewer cats and more native forest within 1km were included in the model but had a weaker association. The second-best model also included small and medium weight exotic prey species as a small positive relationship, along with the devil, cat and critical weight range native prey.

In the top model for summer, quolls were more abundant where there were more stems over 10cm ($p= 0.0046$), more rats and devils and less possums (Table 2-2 and Figure 2-12). Shrub percentage cover had a small positive association while cats had a small negative association. The second model had a Δ AIC of 3.92 indicating strong support for the top model. This second model showed a positive relationship with native forest and plantation within 1km, stems over 10cm and percentage cover of shrubs. Visibility at 25cm was a small negative influence while canopy height was a small positive relationship. Goodness of fit tests indicated good fit of the models to the data for both winter and summer.

The change in bait recipe had a marked influence on detection of quolls in winter. There was a strong association with Bait 1, the original recipe (Intercept -3.39, $p= 1.57 \times 10^{-17})$ with the negative value indicating a loss of attraction with aging over the 21 nights. Lure age was also an influence in the detection of quolls in the summer

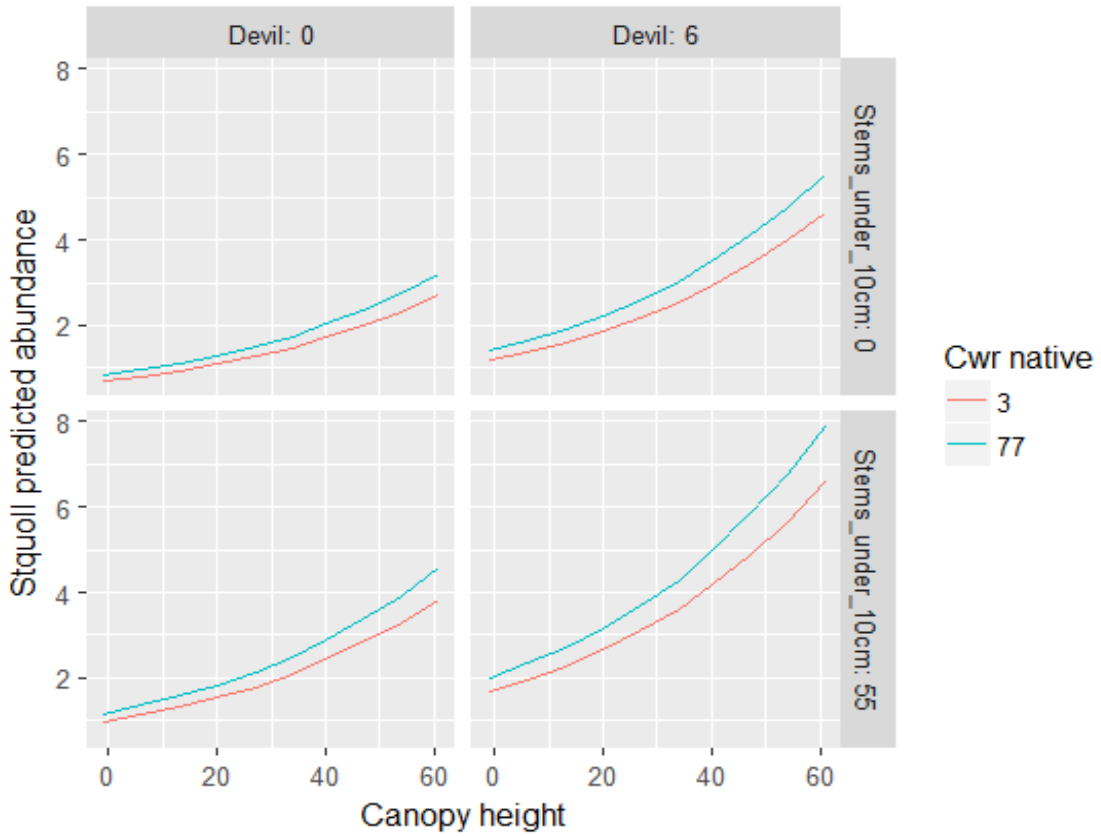

Figure 2-11 Winter estimated abundance of spotted-tailed quolls against canopy height (x-axis), and 10th and 90th quantiles for: number devils (columns), stems under 10cm within 5 m (rows) and critical weight range native animals in red and blue lines

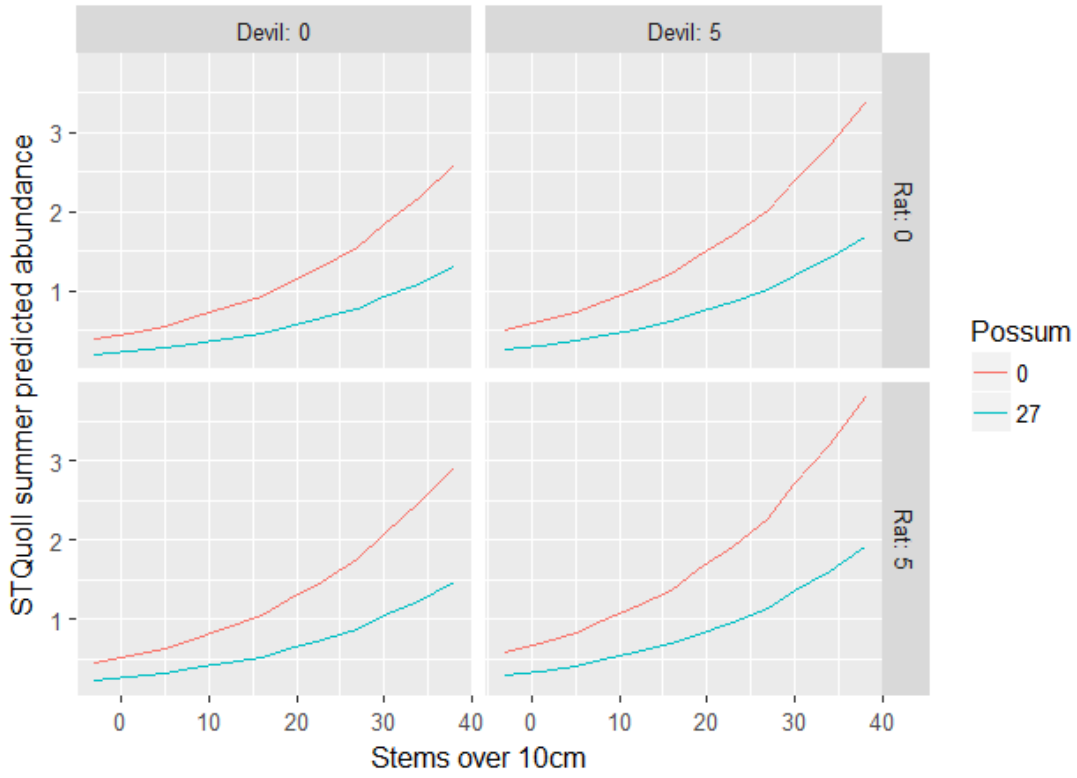

Figure 2-12 Summer estimated abundance of spotted-tailed quolls plotted against the number of stems over 10cm within 5m (x-axis) and 10th and 90th quantiles for: devils (columns), rats (rows) and possums in the red and blue lines respectively

2.3.4 Tasmanian devil abundance modelling

The two best winter models together accumulated 86% of the AIC weight. The next model brought the accumulated AIC weight to 1.00 and had a Δ AIC value of 2.43. These three models were closely aligned and included elevation ($p= 8.49 \times 10^5$), native forest within 1km and presence of quolls, while the top model also included wombats as a strong positive association and stems under 10cm as a weak positive association (Table 2-2 and Figure 2-13). The second-best model is a subset of the first, while the third included critical weight range native prey as a small positive association. Lure age and moon phase influenced detection of devils during winter.

There was only one summer model within a Δ AIC value of 2 and it included the same factors as for winter: elevation, native forest proportion within 1km, presence of wombats ($p=2.28 \times 10^5$) and quolls. This model contributed 97% of the AIC weight (Table 2-2 and Figure 2-14). The second model (Δ AIC 7.68) showed a small positive relationship with road distance and road-use class. Lure age, the round when the camera and lures were set, and the moon phase all appeared as significant detection factors. Goodness of fit tests indicated a good fit of the models to the data for both winter and summer.

Sites where devil facial tumour disease was detected are mapped for winter and summer (Figure 2-15) with the dates when the disease was first recorded at several sites within and in proximity to the study area (Data: Hendricks et al. (2017)). No relationship was noted between the disease occurrence and the habitat variables.

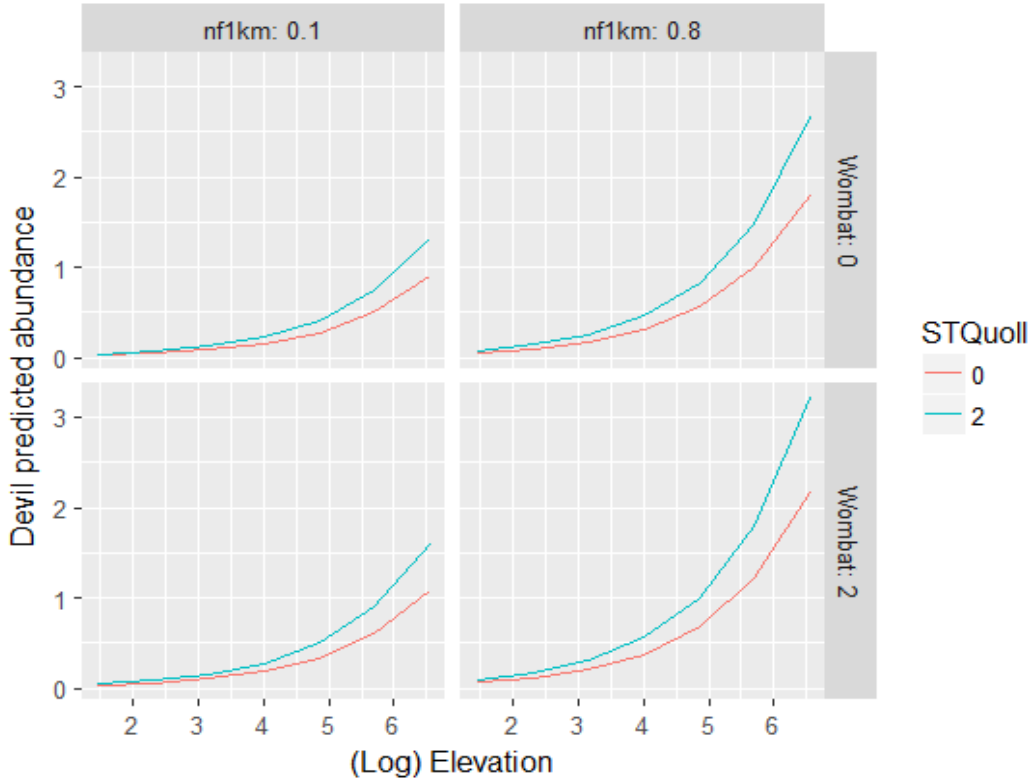

Figure 2-13 Devil winter estimated abundance plotted against log elevation (x-axis,) and 10th and 90th quantiles for: native forest proportion within 1km (columns), wombats (rows) and spotted-tailed quolls in red and blue lines

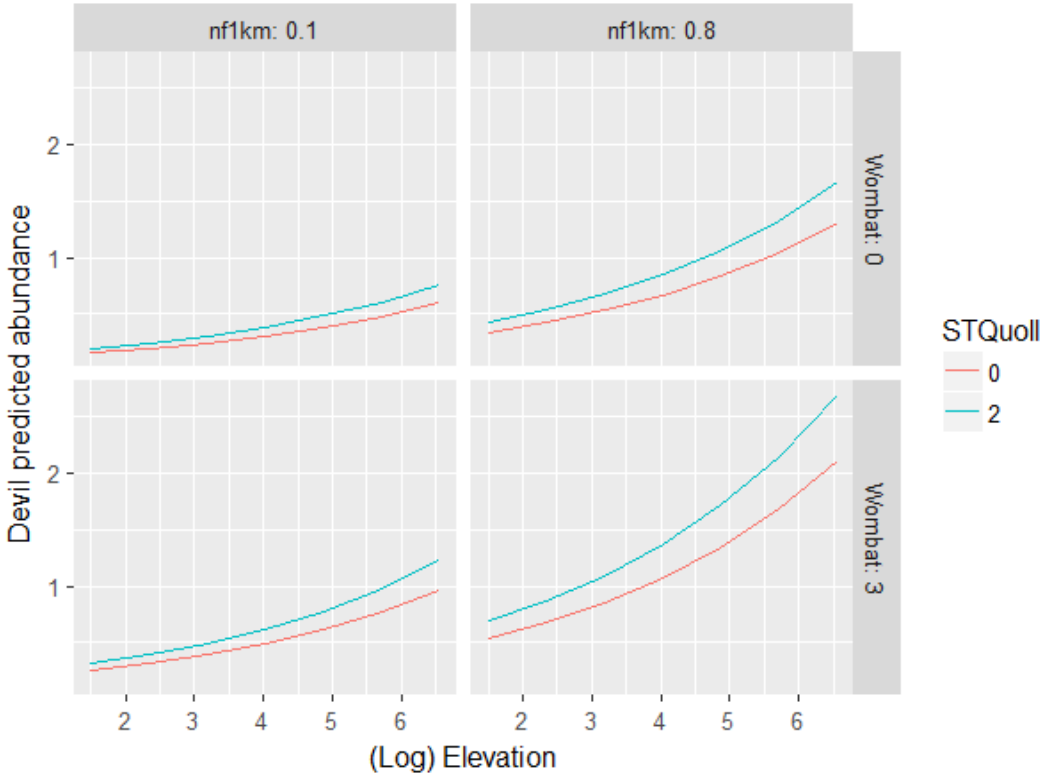

Figure 2-14 Devil summer estimated abundance plotted against log elevation (x-axis,) and 10th and 90th quantiles for: native forest proportion within 1km (columns), wombats (rows) and spotted-tailed quolls in red and blue lines

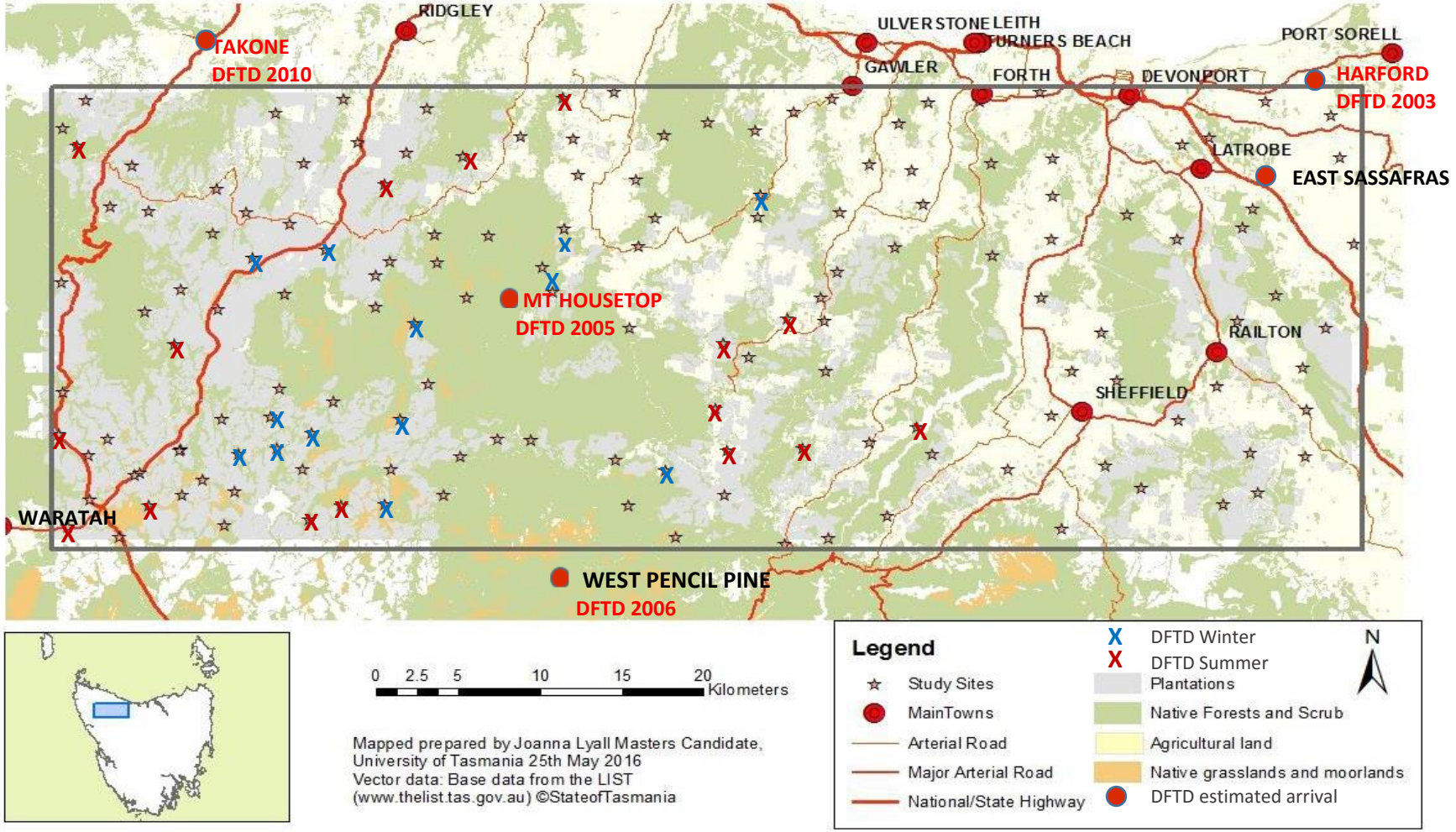

Figure 2-15. Map of study area showing sites where devil facial tumour disease was detected over the winter season (blue crosses) and summer season (red crosses)

2.3.5 Cat abundance modelling

There was only one top model for cats in winter, within 2 Δ AIC (Table 2-2 and Figure 2-16). This model includes more rabbits (p=0.005), critical weight range native prey, more stems under 10cm in diameter within 5m of the site and land-use (positive for agricultural edges and intercept, negative for native grasslands, and native forest and plantation). The proportion of agricultural land within 1km had a small positive association and elevation a small negative association with abundance. Proximity to residential buildings appears in the second model but only as a small effect. Lure age and habitat type were significant detection factors in winter.

During summer, there was again one top model within 2 Δ AIC. This model had an AIC weight of 0.82 and the strongest associated factors included the canopy density (p= 0.021) and presence of devils (p=0.043), with a lesser association with the presence of quolls and elevation, both negative factors (Table 2-2 and Figure 2-17). The presence of small and medium weight exotic prey species and proportion of agricultural land within 1km were both positive although weak associations with cat abundance. The second model (Δ AIC 4.62) identified canopy height as a positive factor and elevation a negative factor while slope, aspect and land use were not significantly related to cat abundance. The factor most strongly associated with the probability of detection was habitat i.e. the location of the site in one of the four habitat/land-use types influenced whether a cat would be detected given it was present. Goodness of fit tests indicated a good fit of the models to the data for both winter and summer.

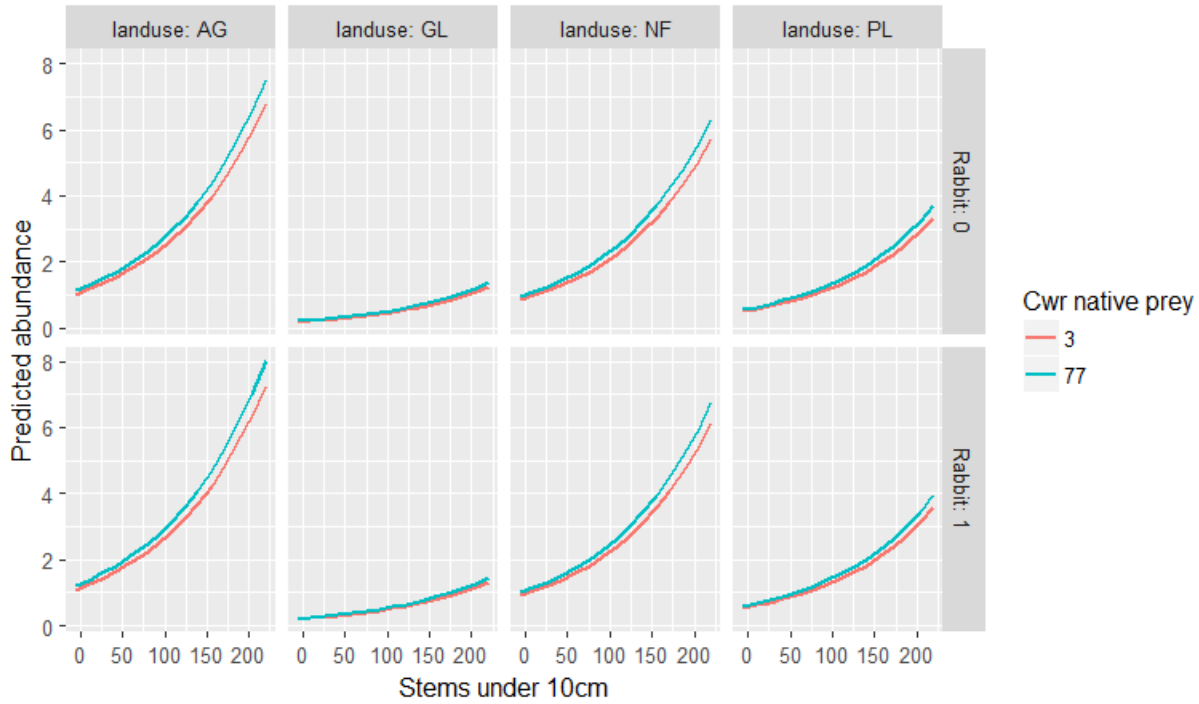

Figure 2-16. Cat winter estimated abundance plotted against stems under 10cm (x-axis), landuse (columns) and 10th and 90th quantiles for: detections of rabbits and critical weight range native prey species (red and blue lines respectively).

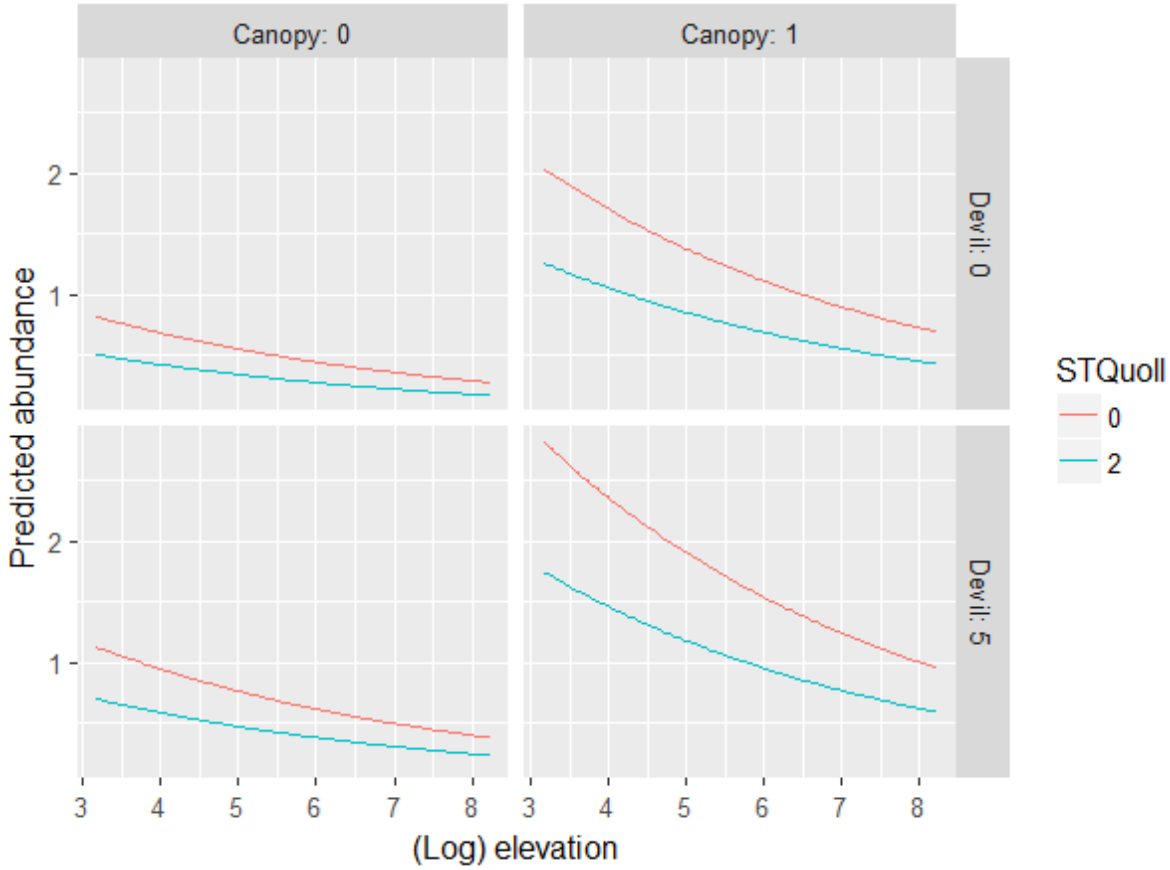

Figure 2-17. Cat summer estimated abundance plotted against (log) elevation, and 10th and 90th quantiles for: canopy density (columns), devil detections (rows), and spotted-tailed quoll detections in red and blue lines respectively

2.4 Discussion

Devils and quolls are of importance within the Tasmanian environment to maintain the ecological function of the forest ecosystems and some top-down pressure on the burgeoning populations of native herbivores. Loss of these predator species could result in large-scale changes to native vegetation communities through over-browsing of understorey species, reminiscent of the collapse of the ecosystems within Yellowstone National Park prior to reintroduction of the top predator, the wolf (Ripple and Beschta, 2003, Ripple and Beschta, 2012). However, there can be unexpected interactions between the top predators and smaller or coexisting predators with flow-on effects to the herbivore populations as found by Palomares et al. (1995) with lynx *Lynx lynx,* when present, controlling numbers of a mesopredator, the Egyptian mongoose *Herpestes ichneumon* which resulted in a greater population of European rabbit *Oryctolagus cuniculus*. This study sought to determine likely factors influencing presence and abundance of the three target species within a highly perturbed landscape.

The results of this study suggest prey species are a factor associated with the presence of quolls,

devils and cats and that the three predators are associated with different landscape factors. The spatio-temporal differences in estimated abundance within and between each of the predators are likely to reflect their individual needs and dictate the specific niches they occupy, and their responses to spatio-temporal changes in food, shelter, breeding and seasonal conditions more broadly.

2.4.1 Spotted-tailed quoll modelling

The distribution of quolls in this study in northwest Tasmania was evidently not related strongly to elevation and presence of wet forest. This is in contrast to results from Glen and Dickman (2011) who found higher abundance of quolls in the dense wet forests of south east mainland Australia and suggested the reason was fewer foxes and therefore less competition from foxes in these relatively intact habitats. Troy (2014) found no relationship in northwest Tasmania between quoll abundance and forest cover or fragmentation despite the presence of the sympatric marsupial predator, the devil. This implies habitat utilization by quolls was not influenced by strong top-down pressure from devils in this prey-rich fragmented landscape. The high population of foxes on the mainland of Australia has resulted in niche contraction for spotted-tailed quolls through competition and predation, while the absence of foxes in Tasmania has meant quolls are able to occupy agricultural land, where they would be absent on the mainland (Troy, 2014)

The results of this study suggest the occurrence of the quoll is strongly associated with the presence of prey within the critical weight range (35g – 7000g). Also, quolls appear more abundant where there are taller forests (plantation and native forest), which may be related to the availability of refuge sites for arboreal prey and denning sites, with denser understorey, that may assist in their mode of predatory behaviour on terrestrial prey (Glen and Dickman, 2006a, Jones et al., 2001, Jones and Barmuta, 2000). Devils and quolls are positively associated. This is likely to be because both species use native forest where there is suitable prey. Where there is suitable reasonably intact native forest and abundant prey, the landscape will support more individuals of both these native carnivores. Saunders (2012) (Honours thesis) also found a positive association between the occupancy and abundance of devils and quolls in a study where she compared rainforest and coastal habitats in northwest Tasmania either in intact wilderness or in closer proximity to agricultural land.

Temporal and spatial partitioning is not examined in this thesis, although these analyses are planned from this camera data set. It is likely some partitioning occurs to avoid direct competition and antagonistic encounters. Temporal partitioning is suggested by the difference in peak movement between quolls and devils, with devils more active during the night and negatively influenced by the moon, while quolls are most active at dusk and dawn (Andersen et al., 2016). There also appears to

be some spatial avoidance. Quoll can partition the habitat vertically by hunting above ground in trees, and by using logs and trees for travelling above ground possibly allowing them to avoid encounters with devils (Jones and Barmuta, 2000, Andersen, 2016). Spatial partitioning between quolls and other carnivores, including in vertical activity, is recorded on the mainland of Australia where there is a strong overlap in diet between the alien red fox and native spotted tailed quoll. Quolls are more arboreally active in forests as a response to direct competition by foxes that prefer to hunt in cleared habitat (Glen and Dickman, 2008, Glen and Dickman, 2011)

Different factors at both a camera site and landscape level appear to be associated with the abundance of quolls in winter compared to summer. The density of understorey and the presence of more trees as noted through the two factors, “stems under 10cm” and “stems over 10cm” diameter, were strong attributes in predicting quoll abundance during these seasons. There is also a strong relationship between the presence of prey species and quoll abundance, particularly during winter. Increased structural complexity where there is more shrubbery provides habitat for the prey species, more cover for hunting and cover for denning for the quolls (Belcher, 1995, Jones and Barmuta, 2000). This habitat complexity may be of critical importance to female quolls that have non-overlapping territories and usually several dens within the core range for breeding and refuge (Troy, 2014, Belcher and Darrant, 2006). The preference for more stems over 10cm DBH (more trees present = structural complexity, including hollows) during summer may be a response to the females’ requirement for denning sites for their young. Quoll mating season is in June, with births in July and young emerge from the pouch and are left in a den from August where they stay until they are weaned in December (Jones and Barmuta, 1998). This dependency of structural complexity for denning coincides with findings elsewhere, such as Beasley and Rhodes (2012) who found raccoon fecundity to be linked to den availability, which is in turn linked to the density of tree cavities providing potential denning sites. Quolls may face similar limitations at a fine spatial scale. Seasonal fluctuations in prey availability and hunting preferences of quolls may result in them hunting arboreally more frequently in summer to coincide with the availability of young hollow-dependent birds and mammals. Breeding of prey species is timed so young are weaned in summer when resources are most abundant, and breeding of the predator species is synchronized with their prey so that young predators are also weaned in summer when naïve juvenile prey are most abundant. Dietary analysis indicates quolls consume the introduced black rats (Andersen et al., 2016), found in disturbed environments on the edges of agricultural land and some native forests and plantations. The rats were more abundant during winter than summer and may become an important food source when other prey species are scarce. The negative relationship with possums was unexpected, as possums are known to be a prey species for the quolls (Jones and Barmuta, 1998), however in this

study possums were in higher densities at agricultural sites where large numbers of possums were observed travelling some distance from cover and this would not be favorable for quoll predatory behaviour.

2.4.2 Tasmanian devil modelling

Detections of devils across my study area indicated a trend in abundance from east to west and between lower and higher elevation. devils were more abundant at higher elevation, where there is more native forest and plantations and less farmland. The impact of the devil facial tumour disease (DFTD) on the population of devils may have contributed to this pattern. When the field work for the study was done (2014 – 2015), the eastern part of the study area had had DFTD for 10 years (since 2003 – 2004). The facial tumour disease spread to the western extremity of the study area around 2008-09 (Hendricks et al., 2017). It takes around six years for populations of devils to decline to very low numbers following disease outbreak (Lachish et al., 2007). This pattern and timing of disease spread is reflected in the detections of diseased devils on the cameras. However, although explaining some of the bias, it would not explain all of the bias. Figure 2-5 indicates there is still a strong population, including all age groups, within the forested areas but fewer throughout the agricultural areas.

Elevation, native forest, presence of quoll and wombats were factors identified as having a strong positive association with occupancy and abundance of devils. Habitat features related to estimated devil abundance included elevation and native forest understorey, while in winter, vegetation as represented by the density of stems under 10 cm, also had a strong association with devil abundance. These factors are closely aligned, as the largest areas of native forest remain at elevation. This finding contrasts with Troy (2014), who found devil abundance increased with decreasing forest cover and increasing fragmentation. This could be explained by less intensive agriculture in her study area leaving more connectivity between the areas of remnant vegetation.

Wombats also feature strongly in predicting the abundance of devils, above any other of the preferred prey species, including Bennett's wallabies and pademelons, but also possums and the critical weight range native prey. With their relatively non-selective diet, including both predation and scavenging, devils find prey throughout the landscape. Paradoxically the major known prey species of the devils, pademelons, did not appear as an explanatory factor in the models but wombats did. There are two suggested explanations for this unexpected relationship with wombats. The first is that the pattern of spread of devil facial tumour disease in relation to the timing of my field work indicates a higher abundance of the devil in the western, and mostly higher elevation parts of my study area. This coincides with larger populations of wombats inhabiting the more open

forests around native grasslands and moorlands (Taylor, 1985). The second possible explanation is that wombats may form a greater component of the diet of devils in this habitat type than previously thought. Dietary studies of scats have shown wombats form a large proportion of the devils diet in this high country which is in close proximity to the study area (Pemberton et al., 2008, Jones and Barmuta, 1998). Wombat density varies within different vegetation types and they are known to be in higher abundance in the open country at elevation than in the coastal areas (Taylor, 1985). The availability of wombats as prey would influence the numbers taken by devils. A recent dietary study of devils by Andersen et al. (2016) found wombats composed 23% of devil scats at Cradle Mountain, which is 15-20 km in a direct line from the southern extent of my study area compared to 2.4% at Arthur River on the west coast. In other sites spread across the State Andersen (2016), found no wombat component within devil scats. Hence the results from the estimated abundance analysis on devils within this study area concur with the findings of Jones and Barmuta (1998) that during summer, large mammal species i.e. wombats, form a greater part of the diet of devils. This is likely to be due to the abundance of young wombats becoming independent at this time of year.

Devils were detected less often with increasing distance from the nearest road, and they were more associated with general access roads. Access roads are often sealed and traverse areas running through bushland, but vehicles traveling at speed result in large numbers of wildlife being killed. Hence the association between detection rates of devils and roads is consistent with the notion that roads may be exploited by devils as an important source of carrion and possibly for travelling. Their attraction to roads is of concern as mortality due to collisions has been found to be the second greatest threat to devil survival after the DFTD (Save the Tasmanian Devil Program).
A factor not investigated in this study potentially influencing the results is that macropod and possum control occurs extensively on farmland in the State. This may limit use of farmland by devils either through loss of prey availability or directly where some landowners may also target devils.

2.4.3 Cat modelling

Cats were found throughout the study area, but were more abundant at lower elevations in the northeast of the study area in proximity to and on the margins of agricultural land, particularly where there have been settlements or other human disturbance in the past. During winter, land use type, density of undergrowth and presence of prey species were the major factors influencing cat abundance, while in summer low elevation and canopy density were the strong influences. My winter season, from May until August, coincides with the start of the rabbit breeding season. Catling (1988) found a functional response to the rabbit breeding season for cats, with a large part of their

diet made up of young rabbits over late winter/spring followed by a change to more invertebrates, reptiles and birds over the summer. While cats may prefer rabbits, they are opportunistic and adaptable, regularly preying on small animals (Spencer et al., 2014) but have been known to attack and kill prey up to 4kg (Fancourt, 2015). Cats are less influenced by habitat factors during the summer as their diet changes with declining availability of young rabbits to being more generalised and opportunistic (Molsher, 2006). The modelling for my study indicates estimated abundance of cats was greater on the edges of farmland, where typically there is a canopy with understorey present, but with low density enabling ease of movement for hunting prey. They preferentially use this interface between pastures and woody vegetation, choosing higher structural complexity (Bengsen et al., 2012, Doherty, 2014). In the Philippines too, the cat is found more often in the transition zone between rainforest and agricultural land. While there was no indication of temporal avoidance of the sympatric civets (*Paradoxurus hermaphroditus* and *Viverra tangalunga),* there was temporal avoidance of dogs and human activity (Bogdan et al., 2016).

Cats also inhabit native forest sites with low understorey density and younger plantation sites (Chapter 3) where presumably the understorey has not yet regenerated. In open country, structural diversity in the form of rocky outcrops or dense understorey allows prey some refuge, which explains the greater hunting success cats have where there is less complexity and understorey cover (McGregor et al., 2015, McGregor et al., 2016, Hohnen et al., 2016). This appears at odds with other studies in more forested areas that find cats prefer cover rather than open habitats to move through (Edwards et al., 2002, Bengsen et al., 2012). However, it is likely they use areas with cover to conceal their approach to more open and disturbed areas for the kill. Prey availability is a key determinant for cats inhabiting these areas, however this can also be influenced by interspecific predation and competition (Doherty, 2014).

2.4.4 Relationships between spotted-tailed quoll, Tasmanian devil and cat

No relationship was found between the abundance of cats and devils or quolls and devils, which may indicate no avoidance behaviours between these species, but there was a reciprocal negative association between the abundance of quolls and cats. Cats do not feature in the models for devils, which is consistent with cats not posing a major threat to devils and that their diets may be sufficiently different to not substantially compete for prey. Devils typically prey upon larger prey than do cats (large prey >7kg) and scavenging is a regular part of their dietary intake, while cats prefer live prey, with a preference for small (<2000g) (Kutt, 2012, Dickman, 1996) but they are occasionally known to prey on animals to 4kg (Fancourt, 2015). There is speculation that devils may exert some top-down pressure on cats resulting in cats actively avoiding devils. This is consistent

with some evidence the decline of devils due to disease is leading to competitive release of cats in some areas of the State (Hollings et al., 2016, Hollings et al., 2013a). Cats have been reported to spatially and temporally avoid devils, even at low densities (Lazenby and Dickman, 2013) and up to 10 years following disease outbreak and the onset of population decline (Fancourt BA, 2015). However, cats co-exist with devils in my study area, and are apparently more abundant where more devils are present, perhaps through segregation of prey resources. But they are likely to be in direct competition with quolls for rabbits and critical weight range native prey and in particular, denning sites. The pademelon and common brushtail possum are also considered prey for cats(Fancourt, 2015)), devils and quolls (Jones and Barmuta, 1998, Glen and Dickman, 2005b) in Tasmania

The presence of sympatric predators is of greater importance to cats during summer than in winter with devils having a positive influence on estimated abundance of cats and quolls a negative influence.

Both the cat and spotted tailed quoll exhibit a negative association to each other. Spatially there appears to be some segregation with quolls more abundant within native forest and cats on the margins of agricultural land. This habitat separation is likely to reduce competitive stress between the species. The negative association of quolls on cats appears stronger where there is a more dense canopy. This suggests there may be stronger competition between the two species within the forest margins where their ranges may overlap and the summer period is when there is most likely to be competition between breeding female cats and quolls for denning sites. Dependence on specific habitat, particularly for reproduction, is found in many specialist predators. Female fishers *Martes pennanti* in British Columbia, Canada select forests with larger diameter trees, more likely to have hollows (Weir et al., 2012). Martens *Martes americana,* Iberian lynx *pardinus* and genets *Genetta genetta*, also seek older and more structurally complex forests for increased availability of denning sites used for shelter, protection from predation and raising young (Potvin et al., 2000, Carvalho et al., 2014, Fernández and Palomares, 2000). Availability of den sites is of particular importance within a disturbed landscape for species using multiple den sites, such as quolls *Dasyurus maculatus*, genets *Genetta genetta*, eastern spotted skunks *Spilogale putorius* and raccoons *Procyon lotor*. Lack of den sites could potentially limit their reproductive capacity (Fernández and Palomares, 2000, Lesmeister et al., 2008, Glen and Dickman, 2006b, Beasley and Rhodes, 2012).

No negative association is seen between devils and quolls. Devils are found in more abundance in native forest at elevation coinciding with the preferred habitat of quolls. Jones and Barmuta (2000) found while the diets of quoll and devil can overlap significantly, the quolls eat considerably more arboreal prey than devils so there is some vertical division in prey location. However there is also a size difference in preferred prey, with adult devils targeting more large prey while the quolls favour

small to medium prey, including birds and reptiles (Jones and Barmuta, 1998, Belcher et al., 2007, Andersen et al., 2016). While this study revealed a strong association between wombats and devil abundance, this has not been demonstrated to be a predator-prey relationship.

2.5 Conclusion

There are significant differences in the relative abundance of devils, quolls and cats across the study area. There are also seasonal differences in their habitat and land use, influenced by breeding cycles, prey preferences and availability. Both devils and quolls are more abundant in native forest while cats are more often found in agricultural areas. Spotted tailed quolls appear more specialised in their habitat requirements than the other two species, and are associated with taller forests and dense understorey, but there is no influence of elevation. The quoll may be restricted to areas supplying the structural complexity required for multiple den sites and opportunities to hunt arboreal prey.

Elevation, native forest cover and prey emerge as the most important factors predicting abundance of devils, the most abundant of the three predators. Interestingly the detection of devils was associated with the presence of wombats. Devils are more flexible in their habitat preferences and diet than either quolls or cats and occupy a significantly larger and wider range of habitats. They have a generalised diet including a high proportion of material obtained by opportunistic scavenging (Pemberton et al., 2008). Prior to the DFTD their population was large and widespread. The consequent loss of a large proportion of their population, in conjunction with abundant prey availability, suggests devils are not restricted by the availability of resources. Further work is needed to see whether the higher abundance of devils associated with wombats and higher elevation is because the devil facial tumour disease has contracted the devil population to these higher elevations where wombats are also more common, or if it is a direct relationship between devils and wombats. The higher abundance of devils in this south west corner of the study area may be a result of the lag time between the DFTD spreading across the study area and depletion of the population. The devil is the top predator since the loss of the thylacine and maintaining their population in the face of the DFTD is important to retain some top-down pressure on the native herbivores.

Cats are highly adaptable to a wide range of habitat types and have become established as a predator on most continents globally. This invasive species is implicated in 26% of extinctions of birds, mammal and reptile species worldwide (Doherty et al., 2016b). Cats will prey upon a wide range of available species but will often specialize by selectively preying upon specific species, often with devastating effects on local populations of that particular species (Doherty et al., 2016a). In this study cats are more abundant on the edges of agricultural land with cover, including trees and

undergrowth, assumed to provide concealment during hunting. Their abundance in winter is influenced by prey availability, as indicated by the strong association with rabbits on farm edges targeted in this study and critical weight range native species. In summer prey does not appear as a factor influencing abundance. Instead, the detection of quolls is a strong negative factor. The possible overlap of habitat, diet and denning requirements, suggests the cats and quolls are in direct competition. This would result in avoidance behaviours between the species, possibly including active avoidance and temporal or spatial separation of the two species. There are many examples of avoidance between mesocarnivores. In north-eastern New South Wales, Australia, the quoll is hypothesised to be in higher abundance in dense forests where there is a low density of foxes. This suggests the quolls are evading direct competition from foxes through spatial avoidance (Glen and Dickman, 2011, Glen and Dickman, 2008). Devils and quolls in far northwest Tasmania use temporal separation to avoid direct competition or aggressive encounters (Andersen, 2016).

Spotted tailed quolls and devils occupy similar habitats, as indicated by the higher relative abundance of these species in some symmetry across the differing land uses. Cats and devils have no adverse influence on each other's presence indicating sympatry across the different landuses, possibly through some spatial or temporal separation. Quolls and cats however, avoid each other or choose different habitats, suggesting there may be direct competition for resources between the two species. They are of similar size, prey on similar sized species and require multiple den sites for shelter and raising young. This relationship between cats and quolls should be explored further to ascertain whether there are spatial or temporal influences, interspecies predation or direct competition for prey and denning sites. Human influence should also be examined to determine how much influence culling of browsing prey species has on the predators and if there is continuing persecution of the native predators. Within the natural and plantation landscapes, management interventions to increase understorey complexity in disturbed habitats may reduce the spread and success of cats while improving occupancy opportunities for the quoll and devil. Quolls in particular, appear vulnerable to displacement where there are cats and native predators competing for resources.

2.6 Appendix – Main survey

Table 2-3 Detections of small prey species <500g by habitat type and season used in the "preysm" grouping which included both native and exotic species, "cwtnative" which includes small and medium native prey species, and "sm_med_exotic" which is a count of small and medium weight exotic species detections

Species	Common name	Avwt (g)	Native/ exotic	Wint AG	Wint GL	Wint NF	Wint PL	Wint Total	Summ AG	Summ GL	Summ NF	Summ PL	Summ Total	Grand Total
Anthochaera paradoxa	Yellow wattlebird	175	Native	0	0	0	0	0	0	0	0	5	5	5
Cercartetus nanus	Eastern pigmy possum	24	Native	0	0	1	0	1	0	0	1	1	2	3
Colluricincla harmonica	Grey shrike thrush	63	Native	2	0	0	0	2	2	0	1	0	3	5
Cracticus tibicen	Australian magpie	285	Native	9	0	0	0	9	17	0	0	0	17	26
Lichenostomus flavicollis	Yellow throated honeyeater	31	Native	0	0	0	0	0	1	0	0	0	1	1
Malurus cyaneus	Superb fairywren	10	Native	0	0	0	0	0	3	1	1	0	5	5
Mus musculus	House mouse	15	Exotic	0	0	0	2	2	0	0	0	0	0	2
Pachycephala pectoralis	Golden whistler	25	Native	0	0	0	0	0	0	0	1	0	1	1
Petaurus breviceps	Sugar glider	125	Exotic	1	0	0	0	1	0	0	0	0	0	1
Phaps chalcoptera	Common bronzewing	317	Native	0	0	4	0	4	1	0	0	1	2	6
Phaps elegans	Brush bronzewing	200	Native	3	0	4	0	7	7	0	5	3	15	22
Platycerus caledonicus	Green rosella	140	Native	0	0	0	0	0	0	0	0	1	1	1
Pseudomys higginsi	Long-tailed mouse	67	Native	0	0	2	0	2	0	0	0	3	0	2
Rattus lutreolus	Swamp rat	122	Native	0	3	1	3	7	0	0	9	0	12	19
Rattus	Black rat	280	Exotic	309	16	104	75	504	237	7	22	27	293	797
Sericornis frontalis	White-browed scrubwren	12	Native	0	1	0	0	1	0	0	0	2	2	3
Sericornis humilis	Tasmanian Scrubwren	18	Native	0	1	1	1	3	0	0	1	0	1	4

Small animal			Native	3	0	3	0	6	1	0	0	1	2	8
Small bird			Native	0	1	1	0	2	0	0	3	0	3	5
Strepera fuliginosa	Black currawong	374	Native	2	0	1	16	19	1	4	10	57	72	91
Strepera versicolor arguta	Clinking currawong	168	Native	2	0	0	0	2	0	0	5	0	5	7
Tiliqua nigrolutea	Blotched bluetongue	500	Native	0	0	0	0	0	0	0	0	1	1	1
Turdus merula	Blackbird	89	Exotic	32	0	0	0	32	173	0	0	1	174	206
Zoothera lunulata	Bassian thrush	100	Native	13	0	4	10	27	12	0	16	7	35	62
Grand total:				376	22	126	107	631	455	12	75	110	652	1283

Table 2-4 Detections of medium prey species >500g and 7000g by habitat type and season used in the "preymed" grouping which included both native and exotic species, "cwrnative" grouping which includes small and medium native prey species, and "sm_med_exotic" which is a count of small and medium weight exotic species detections

Species	Common name	Avwt (g)	Native / exotic	Wint AG	Wint GL	Wint NF	Wint PL	Wint Total	Summ AG	Summ GL	Summ NF	Summ PL	Summ Total	Grand Total
Anas superciliosa	Black duck	1020	Native	1	0	0	0	1	10	0	0	0	10	11
Bettongia gaimardi	Tasmanian bettong	2000	Native	40	0	1	0	52	15	0	2	0	21	73
Calyptorhynchus funereus	Yellow-tailed black cockatoo	700	Native	0	0	0	0	0	1	0	0	0	1	1
Corvus tasmanicus	Forest raven	650	Native	0	0	0	1	1	7	0	0	3	10	11
Hydromys chrysogaster	Rakali/ water-rat	680	Native	3	0	0	0	3						3
Isoodon obesulus	Southern brown bandicoot	775	Native	107	1	19	26	153	13	0	8	10	31	184
Lepus europaeus	European Hare	4000	Exotic	1	0	0	0	1	9	0	0	0	9	10
Medium animal			Native	19	2	11	6	38	8	2	9	18	37	75
Ornithorhynchus anatinus	Platypus	1145	Native	1	0	0	0	1	1	0	0	0	1	2
Oryctolagus cuniculus	European rabbit	1580	Exotic	50	0	7	2	60	68	2	2	3	75	135
Perameles gunnii	Eastern barred bandicoot	640	Native	4	0	0	0	5	3	0	0	2	5	10
Porphyrio	Purple swamphen	950	Native	1	0	0	0	2	0	0	0	0	2	4
Potorous tridactylus	Long-nosed potoroo	1100	Native	115	3	42	43	203	60	3	28	76	167	370
Pseudocheirus peregrinus	Common ringtailed possum	900	Native	5	1	5	0	11	1	0	1	2	4	15
Tachyglossus aculeatus	Echidna	4500	Native	2	2	16	19	39	3	16	45	55	119	158
Thylogale billardierii	Tasmanian pademelon	5450	Native	2398	113	797	714	4036	1804	214	1300	1310	4636	8672
Tribonyx mortierii	Tasmanian native hen	1300	Native	86	0	0	0	100	251	0	0	0	251	351
Trichosurus vulpecula	Common brushtail possum	2875	Native	655	31	102	71	1524	1057	43	125	148	1420	2944
Grand total				3488	153	1000	882	6230	3311	280	1520	1627	6799	13029

Table 2-5 Detections of large prey species > 7000g by habitat type and season detections. Fallow deer are unlikely to be regular prey for the larger predators, hence only native species were included in the "preylg" grouping for analysis

Species	Common name	Avwt (g)	Native/exotic	Wint AG	Wint GL	Wint NF	Wint PL	Wint Total	Summ AG	Summ GL	Summ NF	Summ PL	Summ Total	Grand Total
Dama dama	Fallow deer	57000	Exotic	0	0	0	0	0	2	0	0	0	2	2
Macropus rufogriseus	Bennett's wallaby	16850	Native	20	19	32	52	123	3	36	31	222	292	415
Vombatus ursinus	Common wombat	26000	Native	6	32	2	23	63	6	63	7	28	104	167
Grand total				26	51	34	75	186	11	99	38	250	398	584

Table 2-6 Detections of all predator species by habitat type and season.

Species	Common name	Avwt (g)	Size class	Native /exotic	Wint AG	Wint GL	Wint NF	Wint PL	Wint Total	Summ AG	Summ GL	Summ NF	Summ PL	Summ Total	Grand Total
Accipiter fasciatus	Brown goshawk	454	small	Native								1		1	1
Accipiter novaehollandiae	Grey goshawk - white phase	545	med	Native									1	1	1
Antechinus swainsonii	Dusky antechinus	50	small	Native			1		1						1
Canis lupus familiaris	Domestic dog	16000	large	Exotic	18		2		20	2		3	1	6	26
Dasyurus maculatus maculatus	Spotted-tailed quoll	5500	med	Native	37	10	67	35	149	21	6	53	43	123	272
Dasyurus viverrinus	Eastern quoll	1090	med	Native				3	3		1		5	6	9
Felis catus	Cat (feral & domestic)	4050	med	Exotic	137	12	22	22	193	90	12	15	16	133	326
Sarcophilus harrisii	Tasmanian devil	7000	large	Native	68	54	138	89	349	47	41	99	77	264	613
Sminthopsis leucopus	White-footed dunnart	23	small	Native									1	1	1
Grand Total				**Totals**	260	76	230	149	715	160	60	171	144	535	1250

Table 2-7. Predictor variables used in the estimated abundance modelling with their summary statistics

Variable description	Code used	Summary statistics of raw variables used					
Quoll	**dasyurus**	Min. :0.0000	1st Qu.:0.0000	Median :0.0000	Mean :0.8267	3rd Qu.:1.0000	Max. :7.0000
Cat	**felis**	Min. : 0.000	1st Qu.: 0.000	Median : 0.000	Mean : 1.087	3rd Qu.: 1.000	Max. :13.000
Devil	**sarcophilus**	Min. : 0.00	1st Qu.: 0.00	Median : 0.00	Mean : 2.06	3rd Qu.: 3.00	Max. :14.00
Bennett's wallaby	**macropus**	Min. : 0.0	1st Qu.: 0.00	Median : 0.00	Mean : 0.82	3rd Qu.: 0.00	Max. :18.00
Rabbit	**oryctolagus**	Min. : 0.0	1st Qu.: 0.0	Median : 0.0	Mean : 0.4	3rd Qu.: 0.0	Max. :18.0
Wombat	**vombatus**	Min. :0.0	1st Qu.:0.00	Median :0.00	Mean :0.42	3rd Qu.:0.00	Max. :8.00
Pademelon	**thylogale**	Min. : 0.00	1st Qu.: 3.00	Median : 7.50	Mean : 26.87	3rd Qu.: 19.00	Max. :909.00
Brushtail possum	**trichosurus**	Min. : 0.00	1st Qu.: 0.00	Median : 1.00	Mean : 10.17	3rd Qu.: 6.00	Max. :632.00
Black rat	**rrattus**	Min. : 0.00	1st Qu.: 0.00	Median : 0.00	Mean : 3.36	3rd Qu.: 1.00	Max. :59.00
Blackbird	**turdus**	Min. :0.0000	1st Qu.:0.0000	Median :0.0000	Mean :0.2133	3rd Qu.:0.0000	Max. :8.0000
Small prey	**preysm**	Min. : 0.000	1st Qu.: 0.000	Median : 0.000	Mean : 4.207	3rd Qu.: 3.000	Max. :60.000
Medium prey	**preymed**	Min. : 0.00	1st Qu.: 6.00	Median : 13.00	Mean : 41.53	3rd Qu.: 36.00	Max. :955.00
Large prey	**preylg**	Min. : 0.00	1st Qu.: 0.00	Median : 0.00	Mean : 1.24	3rd Qu.: 1.00	Max. :18.00
Critical weight range native species	**cwtnative**	Min. : 0.00	1st Qu.: 6.25	Median : 14.00	Mean : 41.74	3rd Qu.: 35.75	Max. :955.00
Small-medium exotic species	**sm_med_exotic**	Min. : 0.00	1st Qu.: 0.00	Median : 0.00	Mean : 4.00	3rd Qu.: 2.75	Max. :60.00
Predators large and medium	**predlgmed**	Min. : 0.000	1st Qu.: 1.000	Median : 3.500	Mean : 4.353	3rd Qu.: 6.000	Max. :23.000
Building use	**build_use**	Non-residential:70	Residential :80				
Building distance	**build_dist**	Min. : 50.1	1st Qu.: 292.8	Median : 749.8	Mean :1384.9	3rd Qu.:2136.1	Max. :6345.5
Proportion agricultural land at 1km	**ag1k_prop**	Min. :0.0000	1st Qu.:0.0000	Median :0.0800	Mean :0.2525	3rd Qu.:0.4975	Max. :0.9600
Proportion native forest at 1km	**nf1k_prop**	Min. :0.0000	1st Qu.:0.1800	Median :0.3100	Mean :0.3758	3rd Qu.:0.5700	Max. :1.0000
Proportion plantation forest at 1km	**pl1k_prop**	Min. :0.0000	1st Qu.:0.0300	Median :0.2950	Mean :0.3371	3rd Qu.:0.6075	Max. :0.9800
Proportion of negligible mature habitat at 1km	**mhprop1kneg**	Min. :0.2263	1st Qu.:0.8489	Median :0.9457	Mean :0.8799	3rd Qu.:0.9969	Max. :1.0000

Proportion of low quality mature habitat at 1km	**mhprop1klow**	Min. :0.000000	1st Qu.:0.001075	Median :0.033950	Mean :0.081423	3rd Qu.:0.092600	Max. :0.560300
Proportion of medium quality mature habitat at 1km	**mhprop1kmed**	Min. :0.00000	1st Qu.:0.00000	Median :0.00000	Mean :0.01270	3rd Qu.:0.01273	Max. :0.17600
Proportion of high quality mature habitat at 1km	**mhprop1khigh**	Min. :0.000000	1st Qu.:0.000000	Median :0.000000	Mean :0.025652	3rd Qu.:0.008425	Max. :0.419300
Landuse categories	**landuse**	AG:44	GL:15	NF:46	PL:45		
River size groupings	**rivgroups**	Large : 19	Medium: 14	Small :117			
Distance to closest river	**rivdist**	Min. : 0.14	1st Qu.: 22.14	Median : 83.63	Mean :124.81	3rd Qu.:180.47	Max. :678.72
Road use class groupings	**rduseclass**	Access:94	Hway :17	Track :39			
Distance to closest road	**rddist**	Min. : 0.68	1st Qu.: 31.57	Median : 67.23	Mean :118.95	3rd Qu.:167.39	Max. :671.39
Number of stems >10cm	**totstemoverten**	Min. : 1.00	1st Qu.: 7.00	Median :11.00	Mean :12.05	3rd Qu.:16.00	Max. :34.00
Number of stems <10cm	**totstemunderten**	Min. : 0.00	1st Qu.: 4.00	Median : 17.50	Mean : 26.16	3rd Qu.: 36.75	Max. :200.00
Visual obstruction at cat/quoll height	**visob25**	Min. :0.0100	1st Qu.:0.3425	Median :0.5000	Mean :0.5045	3rd Qu.:0.6575	Max. :0.9800
Visual obstruction at devil height	**visob50**	Min. :0.0300	1st Qu.:0.4325	Median :0.5700	Mean :0.5656	3rd Qu.:0.7300	Max. :0.9900
Visual obstruction at Bennett's wallaby height	**visob100**	Min. :0.0600	1st Qu.:0.5025	Median :0.6800	Mean :0.6502	3rd Qu.:0.8100	Max. :0.9900
Canopy height	**canopyht**	Min. : 4.00	1st Qu.:15.25	Median :25.00	Mean :26.65	3rd Qu.:30.00	Max. :60.00
Aspect	**aspect**	E:33	N:39	S:39	W:39		
Canopy cover %	**canopy**	Min. :0.0500	1st Qu.:0.3000	Median :0.3000	Mean :0.3823	3rd Qu.:0.5750	Max. :0.8000
Log cover	**logs**	Min. :0.00000	1st Qu.:0.01000	Median :0.02000	Mean :0.07553	3rd Qu.:0.10000	Max. :0.80000
Elevation	**elevation**	Min. : 6.0	1st Qu.:212.5	Median :401.0	Mean :380.4	3rd Qu.:551.8	Max. :675.0
Slope	**slope**	<15 :22	>45 : 3	15-30:82	30-45:43		

Table 2-8 Site and detection variables including details for camera and lure settings, set and retrieval dates and season and site coordinates

FACTOR	DESCRIPTION	CODE
CAMERA:	Unique identification number assigned to each camera by University of Tasmania	
START:	Camera set date	00/00/0000
RETRIEVE:	Camera retrieval date	00/00/0000
IMAGENUM	Number of images collected from site. Greater than 600 images= large file	
DEPLOYMENT	Round within the "winter" and "summer" survey seasons	WR1, WR2, WR3 SR1, SR2, SR3
SEASON	Autumn/winter 2014; Spring/summer 2014/15	W S
CAMERASET:	(winter): Rapidfire, 10shots/3sec gap, 10shots/1sec gap, 5shots/1sec gap (summer): Rapidfire	Rapidfire (3x<1sec), 10x3sec, 10x1sec, x1sec
WAYPOINT	GPS waypoint indicating site ID	
LURETYPE:	(winter): Bait 1 (Tuna oil, rolled oats, peanut butter, sardines); Bait 2 (Rolled oats, sardines doubled, peanut butter); Bait 3 (New tuna oil with blood, rolled oats, peanut butter, sardines) (summer): Bait 1	B1,B2,B3
VISLURE:	Visual lure	CD
CAMOP:	Whether camera operational at retrieval	Y/N

Table 2-9 Habitat variables collected for each site with explanations of categories

FACTOR	DESCRIPTION	CODE
SITE:	A random number with the prefix corresponding to habitat type (**A**griculture, **N**ative forest, **P**lantation, Native **G**rasslands/moorland)	A, N, P, G
SPECIES DETECTED	Number of detections of different species at each site including “dasyurus", "felis", "sarcophilus", "thylogale", “trichosurus", "potorous”, “rrattus", "turdus", "isoodon”, “macropus", "oryctolagus", "vombatus", "bettongia"	
GROUPED SPECIES	"bosovis"(combined bos and ovis presence), "preysm", "preymed", "preylg", "cwtnative", "cwtexotic”, “predlgmed"	preysm(<500g) preymed(500g to
BEHAVIOURS	“Investigating/bait/camera”, “Ground scenting”, “Air scenting/listening”, “Travelling”, “Marking”, “Foraging/drinking”, “Scratching/grooming”,“Interacting”	
HABITAT:	**A**griculture, **N**ative forest, **P**lantation and Native **G**rasslands/moorland	AG, NF, PL, GL
SUBHABITAT	Agriculture Scrubby grasslands Native Poa grasslands Buttongrass grasslands Native forest – wet Native forest – dry Hardwood plantation Softwood plantation Mixed hardwood/softwood	ag sc ng bg wf df ph ps mhs
EASTING:	Grid Ref location GDA94 MGA55	
NORTHING:	Grid Ref location GDA94 MGA55	
ELEVATION:	metres asl	(m)
ASPECT:	Compass point	N ,E, S, W
SLOPE:	1=Flat; 2=Gentle; 3=Moderate; 4=Steep	0-15%; 15-30%; 30-45%; 45+
TASVEG:	Interpretation of dominant vegetation as per Tasmanian Vegetation Monitoring and Mapping Program (TVMMP)	
MICROHABITAT:	Specific features noted at camera site e.g site beside stream or in small gully	
CANOPYHT:	Average height estimate of canopy trees (m) at camera site	(m)
SHRUBHT:	Average height estimate (m) of sub canopy and shrub layer (m) at camera site	(m)
GROUNDHT:	Average height estimate (m) ferns, saggs, grasses, mosses at camera site	(m)
CANOPY:	% canopy cover converted to proportion	proportion
SHRUB:	% shrub cover converted to proportion	proportion
GROUND:	% ground cover converted to proportion	proportion
LOG:	% log cover converted to proportion	proportion
ROCK:	% rock cover converted to proportion	proportion
VISOB25: VISOB50: VISOB100:	Visual obstruction (N,E, S,W at 25cm, 50cm, 100cm): Converted % of sight sheet visible to then averaged the four compass points for each height	proportion

PHYSOB (N5M 0-10CM; 10-30CM; 30-50CM; 50-100CM); PHYSOB (N4M 0-10CM; 10-30CM; 30-50CM; 50-100CM); PHYSOB (N3M 0-10CM; 10-30CM; 30-50CM; 50-100CM); PHYSOB (N2M 0-10CM; 10-30CM; 30-50CM; 50-100CM)	Phys. Obstruction – touching or not touching (N, E, S, W in 1m increments, from 5m to 2m at 0-10cm; 10-30cm; 30-50cm; 50-100cm): 1 or 0	proportion
PHYSOB (E5M 0-10CM; 10-30CM; 30- 50CM; 50-100CM); PHYSOB (E4M 0-10CM; 10-30CM; 30- 50CM; 50-100CM); PHYSOB (E3M 0-10CM; 10-30CM; 30- 50CM; 50-100CM); PHYSOB (E2M 0-10CM; 10-30CM; 30- 50CM; 50-100CM)	Phys. Obstruction – touching or not touching (N, E, S, W in 1m increments, from 5m to 2m at 0-10cm; 10-30cm; 30-50cm; 50-100cm): 1 or 0	proportion
PHYSOB (S5M 0-10CM; 10-30CM; 30- 50CM; 50-100CM); PHYSOB (S4M 0-10CM; 10-30CM; 30- 50CM; 50-100CM); PHYSOB (S3M 0-10CM; 10-30CM; 30- 50CM; 50-100CM); PHYSOB (S2M 0-10CM; 10-30CM; 30- 50CM; 50-100CM)	Phys. Obstruction – touching or not touching (N, E, S, W in 1m increments, from 5m to 2m at 0-10cm; 10-30cm; 30-50cm; 50-100cm): 1 or 0	proportion
PHYSOB (W5M 0-10CM; 10-30CM; 30-50CM; 50-100CM)PHYSOB (W4M 0-10CM; 10-30CM; 30-50CM; 50-100CM); PHYSOB (W3M 0-10CM; 10-30CM; 30-50CM; 50-100CM); PHYSOB (W2M 0-10CM; 10-30CM; 30-50CM; 50-100CM)	Phys. Obstruction – touching or not touching (N, E, S, W in 1m increments, from 5m to 2m at 0-10cm; 10-30cm; 30-50cm; 50-100cm): 1 or 0	proportion
5M0TO10CM; 5M10TO30CM; 5M30TO50CM; 5M50TO100CM; 4M0TO10CM; 4M10TO30CM; 4M30TO50CM; 4M50TO100CM 3M0TO10CM; 3M10TO30CM; 3M30TO50CM; 3M50TO100CM 2M0TO10CM; 2M10TO30CM; 2M30TO50CM; 2M50TO100CM	Added physical obstructions for each height for each direction around site at each distance, and converted to a proportion	Proportion
AVPHYSOB0TO10 AVPHYSOB10TO30 AVPHYSOB30TO50CM AVPHYSOB50TO100	Averaged the results of the physical obstructions (5m from camera site to 2m) across the distances to give proportion of area with physical obstruction at each height	proportion
STEMSOVER10 STEMSNUNDER10	Stem density (Number of stems N ,E, S, W for >10cm and <10cm):	number
TOTSTEMOVER10 TOTSTEMUNDER10	Stems totalled for the four compass points around camera site for >10cm and <10cm	Total number
RDCLASS	Road/track class	Accesrd Arterial rd Feeder

		Major arterial rd National/State highway Railway Vehicular track
RDUSECLASS	Nationa highways/feeders/arterial roads Access roads Vehicular track Railway	1 2 3 4
RDSURF	Road/track surface	Sealed Unsealed
RDDIST	Road/track distance from site	Metres (m)
RIVORD	River/watercourse order (small stream to large river)	1-7
RIVDIST	River/watercourse distance from site	Metres (m)
BUILD_TY	Building type	Unknown Rural Small Shed Residence Shed Community Remote shed Public toilet Ruin
BUILD_USE	Indicator of frequency of use	Residential Non-residential
BUILD_DIST	Distance of building from site	Distance (m)
AG1K_EDGE_AREA NF1K_EDGE_AREA GL1K_EDGE_AREA PL1K_EDGE_AREA	agricultural edge to area ratio within 1km buffer native forest edge to area ratio within 1km buffer native grasslands edge to area ratio within 1km buffer plantation edge to area ratio within 1km buffer	edge(m):area(m^2)
AG3K_EDGE_AREA NF3K_EDGE_AREA	agricultural edge to area ratio within 3km buffer native forest edge to area ratio within 3km buffer	edge(m):area(m^2)
GL3K_EDGE_AREA PL3K_EDGE_AREA	native grasslands edge to area ratio within 3km buffer plantation edge to area ratio within 3km buffer	
AG5K_EDGE_AREA NF5K_EDGE_AREA GL5K_EDGE_AREA PL5K_EDGE_AREA	agricultural edge to area ratio within 5km buffer native forest edge to area ratio within 5km buffer native grasslands edge to area ratio within 5km buffer plantation edge to area ratio within 5km buffer	edge(m):area(m^2)
AG1KM_PROP NF1KM_PROP GL1KM_PROP PL1KM_PROP	proportion of agricultural land within 1km buffer proportion of native forest within 1km buffer proportion of native grasslands within 1km buffer proportion of plantation within 1km buffer	proportion

AG3K_PROP NF3K_PROP GL3K_PROP PL3K_PROP	proportion of agricultural land within 3km buffer proportion of native forest within 3km buffer proportion of native grasslands within 3km buffer proportion of plantation within 3km buffer	proportion
AG5K_PROP NF5K_PROP GLK_PROP PL5K_PROP	proportion of agricultural land within 5km buffer proportion of native forest within 5km buffer proportion of native grasslands within 5km buffer proportion of plantation within 5km buffer	proportion
1K_MH_NSUITABLENEG **1K_ MH _LOW** **1K_ MH _MED** **1K_ MH _HIGH**	Mature Habitat Availability (MHA): Within 1K buffer Within 3K buffer	Sqm area
3K_ MH _NSUITABLENEG **3K_ MH _LOW** **3K_ MH _MED** **3K_ MH _HIGH**		
MHPROP1KNEG MHPROP1KLOW MHPROP1KMED MHPROP1KHIGH	Mature Habitat Availability (MHA): Within 1K buffer	Proportions
MHPROP3KNEG MHPROP3KLOW MHPROP3KMED MHPROP3KHIGH	Mature Habitat Availability (MHA): Within 3K buffer	Proportions

Chapter 3 Attributes within plantations in Northwest Tasmania influencing use by spotted-tailed quolls, Tasmanian devils and cats

3.1 Introduction

Human population growth continues to lead to habitat fragmentation and loss, driving the decline of many species worldwide (Wilcove et al., 1998, Wang and Macdonald, 2009, Karanth et al., 2011, Prugh et al., 2009, Fahrig, 2003, Pimm et al., 2014). The extent and pace of changes to natural vegetation cover due to human activity has been increasing for 300 years, but has accelerated over the last 30 years (Scientific Steering Committee of the Land-Use/Cover Change (LUCC) Project, 2006). Over this period the global forest cover has declined by 3.1 percent to just under 4.0 billion ha (Keenan et al., 2015). Land clearance has predominantly been for food, freshwater, fibre, and medicinal products (Ramankutty et al., 2006), with logging and industrial scale agriculture resulting in the greatest areas cleared. For instance the establishment of oil palm plantations in Indonesia and Malaysia had by 2011 resulted in a reduction of forested land by 30% and 20% respectively (Wicke et al., 2011). Similarly, in Amazonian rainforests, forests have been cleared for cattle ranching, logging and more recently soybean production, which has reduced, fragmented and degraded the forested area. The deforested area of the Brazilian Amazon increased from 10 million ha to more than 60 million ha between the 1970s and 2000 (Ramankutty et al., 2006).

Plantation monocultures, replacement of native forests by plantations and the industrial scale of many plantations is of environmental concern due to their contribution to the loss of biodiversity (Brockerhoff et al., 2008). Globally, of the over 8600 listed threated species, the most critical threats have been identified as over-exploitation (which includes logging, hunting and fishing) and agriculture (crop farming, livestock farming and timber plantations) (Maxwell et al., 2016). Apex carnivores are particularly vulnerable to human induced environmental change because they are typically large-bodied, are hypercarnivores and require extensive areas to provide their obligate vertebrate prey resources (Weber and Rabinowitz, 1996, Terborgh, 1992). As a consequence, these apex predators have been extirpated from most continents (Pimm et al., 2014).

Apex carnivores play a key role in maintaining ecosystem services (Ripple and Beschta, 2012, Elmhagen et al., 2010, Terborgh et al., 2001), exerting top-down control on other species through direct predation but also by causing fear of predation. Their decline can lead to trophic cascades and loss of biodiversity (Estes et al., 2011). This disruption can involve increased predation on populations of native prey species by generalist and opportunistic predators, including alien and invasive predators, as a result of mesopredator release (May and Norton, 1996, Andrén, 1988). Invasive predators are often highly adaptable, able to use a wide range of prey as well as disturbed and simplified landscapes.

While it is recognised in Australia that timber plantations, typically eucalypt or pine, do not replicate

the complexity of native forest, they can provide some habitat for carnivore species. The biodiversity value of timber plantations is thought to be related to the prior history of the landscape, proximity to retained native vegetation and the structural complexity of the understorey, including large woody debris, which can be manipulated and enhanced through appropriate forest practices. Establishing plantations on agricultural land where few paddock trees remain can raise the biodiversity value of these simplified landscapes (Kavanagh et al., 2007, Grimbacher, 2011). The conversion to plantation results in a more complex vegetation structure and enhanced connectivity between forest patches at a landscape scale, both of which support more prey and therefore predators. In contrast, conversion of native forest to monoculture plantation results in simplification of the landscape and reduced biodiversity, although plantations still have some biodiversity value (Bremer and Farley, 2010, Brockerhoff et al., 2008, Kanowski et al., 2005). Negative effects of conversion of native forest to plantation can include an increase in invasive species and loss of habitat features (e.g. tree hollows, dense understorey, logs) that are important for hunting and denning (Lindenmayer and Hobbs, 2004, Grimbacher, 2011). Stream-side reserves and other areas of native vegetation retained for non-wood values (e.g., threatened species, visual landscape values, cultural heritage) during the establishment of a plantation, can contribute to the persistence of native species in the plantation either by facilitating recolonisation following conversion or by providing essential habitat features (Grimbacher, 2011). Retention of logs and debris following logging also contribute to structural complexity of the plantation and may be important for predator species. For example, plantations in Scotland provide poor denning opportunities for pine martens *Martes americana* due to loss of the large woody debris typical of mature forests (Caryl et al., 2012).

Structural complexity can influence hunting, shelter and denning opportunities for mammalian carnivores. This complexity is derived in part from the original land use, and from subsequent management, including species composition of plantation, density of planting, age of plantation, rotation number, whether windrows are retained and the composition of windrows (native logs, plantation slash or a combination of both) (Bremer and Farley, 2010, Carnus et al., 2006, Brockerhoff et al., 2008, Stevenson, 2006). These habitat attributes result in variation in the density and type of understorey, the availability of den sites and habitat for prey species. Windrows composed of native logs generally include larger logs and logs with hollows, that persist for decades. In contrast, logs derived from clear-felling of plantations are smaller, have few if any hollows and generally rot more rapidly than the original native logs.

Native vegetation in Tasmania has undergone extensive anthropogenic change since European settlement in the early 1800s (Michaels et al., 2010, Robson, 1983). Initially, native vegetation loss was predominantly for the establishment of agricultural land, however between 1996 and 2011,

following the Tasmanian Regional Forest Agreement (1997), the area of eucalypt plantation in the State increased by 74% to 233,000 hectares and softwood plantations by 6% to 75600 hectares (Forest Practices Authority, 2012b). While both soft and hardwood plantations were established during this period, the extent of eucalypt plantations in particular expanded rapidly across the State. The majority of this expansion was through conversion of native forest to plantations. For example, between 1999 and 2011, 95,690 ha of plantation was established through conversion of native forest (Forest Practices Authority, 2012a), however some plantation was also established on existing agricultural land (Forest Practices Authority, 2012a).

Within this perturbed landscape Tasmania retains an almost intact marsupial predator guild.

This guild includes the two largest extant carnivorous marsupials, the spotted-tailed quoll *Dasyurus maculatus maculatus* and the Tasmanian devil *Sarcophilis harrisii*, existing only in Tasmania and the focus of this study. The eastern quoll *Dasyurus viverrinus* is a smaller member of the marsupial predator guild but is scarce within the study area. The other smaller members of this guild include the dusky antechinus *Antechinus swainsonii,* swamp antechinus *Antechinus minimus,* Tasman Peninsula dusky antechinus *Antechinus vandycki* sp. *nov*. and white-footed dunnart *Sminthopsis leucopus.*

In addition, also established in Tasmania is the placental domestic/feral cat *Felis catus,* an adaptable and opportunistic species contributing more to species decline and extinction world-wide than any other species (Doherty et al., 2016b). Devil populations have undergone widespread and severe decline since the mid-1990s from facial tumour disease (DFTD) (Hawkins et al., 2006, Hawkins, 2009), resulting in losses of up to 95% of the population in some areas (Hollings et al., 2013a). DFTD is a clonally transmissible cancer spread through transmission of live cancer cells. An infected individual biting another transmits the disease through the bite wounds (Hamede RK, 2015). The loss of a large percentage of the population of the apex predator is likely to have consequences for the populations of mammalian carnivores in Tasmania. Habitat is not the limiting factor for devils, although any perturbations to habitat with the potential to impact devil populations are of perhaps greater concern given their endangered status. For instance, adult devils are believed to hold a single den for life, so disturbance at the den site can result in population destabilisation (Owen and Pemberton, 2005). Spotted-tailed quoll, also a threatened species, is a specialised forest predator and with much of its prey being arboreal, the species is an adept climber, using fallen timber and logs for both travel and denning (Glen and Dickman, 2006b). It uses multiple maternal dens located in burrows, rock crevices and hollows in logs or trees. Quolls are likely to be at higher risk than the devils through loss or disruption to habitat. In contrast, the cat will exploit a diverse range of

habitats but is also highly adaptable and opportunistic in its diet, preying on small mammals, insects, birds, reptile and amphibians (Coman and Brunner, 1972, Read et al., 2001, Doherty, 2014). Cats being of similar size to quolls pose a direct threat through competition for habitat and prey.

The overall aim of this study is to determine what plantation types and features of plantations in Tasmania, influence the presence and abundance of native and alien mammalian predators. The purpose is to provide better information to managers to improve the value of plantations for wildlife, in particular the native predators. The quoll, devil, and cat are all known to use plantations, but the degree that they use them and the elements of the vegetation and landscape influencing their use have not been previously investigated. Both the quoll and devil are listed as threatened under the Commonwealth Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act) and Tasmanian Threatened Species Protection Act 1995. The study seeks to answer the following specific questions:

1. At a landscape level, what types and attributes of plantations are associated with greater abundance of native predators, the devil and the quoll?

2. At a site level, what structural elements and attributes of plantations are associated with the abundance of native and alien (cat) predators, within plantations?

3.2 Methods

3.2.1 Study area

The study was conducted in a mixed landscape of native forest, plantation and agriculture of approximately 250,000 ha in Northwest Tasmania, bounded in the south west by the small hamlet of Waratah, and in the north east by Harford, a farming locality (Figure 3-1). Elevation ranged from 6m near the coast to 675m above sea-level in the south of the area, reflected in ranges of annual mean maximum temperatures of 16.9^{O}C on the coast (Devonport Airport) to 12.3 ^{O}C in the southwest (Waratah) and average annual rainfalls of 898mm in the northeast (East Sassafras) to 2,180 mm in the southwest (Waratah) (Bureau of Meteorology). The study area included 47,000 ha of plantation (approx. 40,000 ha hardwood and 7,000 ha softwood), 77,000 of native forest and 82,600 ha of non-forest, consisting mostly of agricultural land (approx. 70,000 ha) and a small area of native grasslands and moorlands (approx. 4500ha). Approximately 13,700 ha of the plantation area was converted from native forest to plantation between 1996 and 2016, an increase in plantation area within the study area of almost 30% (Forestry Tasmania and Private Forests Tasmania, 2016).

Figure 3-1 Location of plantation sites across the study area, shown as white circles. Pale green indicates cleared agricultural land, dark green is predominantly native forest. Plantations at various stages in management can be seen as a patchwork effect particularly in the southwest.

Two surveys were undertaken: from May to August 2014 (winter) and from November to January 2014/2015 (summer). I used 45 sites located in plantations across the study area to assess specific features of plantations used by the three predator species. These sites were nested within the larger, whole of landscape study in Chapter 2. The full set included 300 potential sites, distributed across each of four vegetation/land use types (90 in each of native forest, plantation and agricultural land, with 30 in native grassland/moorlands). These were randomly generated using GIS (ArcGIS 9.3). There was no selection for plantation size, age or species. To ensure the sites were accessible in all weathers, potential sites were located within a 500m buffer placed around all the roads and tracks in the study area. Sites were assigned a unique number in the nested design. From these, 150 sites were selected for the survey, allowing for attrition in site selection at both GIS and field stages. Potential sites were checked visually in map view. Sites close to the edges of adjoining vegetation and land use types were discarded, and in cases where two sites were within 1 km of another, one was discarded to maintain at least 1 km separation of survey sites and if topography proved unsuitable, vehicular access was restricted (for example, by fallen trees over the track) or if vegetation cover had changed since the most recent GIS map layer. Potential sites on the list were

visited until the required number of sites was reached. These sites were randomly divided into three groups to be surveyed in three consecutive rounds. Sites were visited in March 2014 to check accessibility and the first surveys began in May 2014.

The random site selection resulted in two plantation species and a range of age classes particularly among the *Eucalyptus nitens* plantations. This is likely to have influenced the usage of the sites by the three target species. Selecting sites within a smaller age range would reduce confounding factors and may result in clearer results from the site and landscape factors investigated within these plantations.

The mean distance between plantation sites was 2587 m (median 2474 m) with a maximum of 5413 m and minimum of 1232 m. Thirty-seven of the plantation sites were planted with *Eucalyptus nitens* and the remaining eight were *Pinus radiata.* Thirty-eight of the plantation sites, including the 8 *P. radiata* sites, were established through native forest conversion while 7 *E. nitens* plantations were established on agricultural land. The plantations ranged from 1 year to 28 years since establishment. No two plantation sites were situated within the same coupe although due to the greater number of plantation coupes in the south-western corner of the study area, more of the plantation sites were in this sector. Harvesting of native forest for conversion to plantation on State forest ceased on 1 June 2007 (Forest Practices Authority, 2012b). The major differences observed among these plantation sites were the variation in structural complexity resulting from differences in the original land-use, the plantation species, the density of planting and the age of the plantation. In particular, variation in the density and diversity of understorey, and presence of native windrows were thought to potentially influence potential den sites and shelter for the target species, and habitat for prey species. The presence/absence and composition of windrows within the plantations were recorded. Twenty-two sites had windrows composed of native timber logs and 8 with plantation timber and slash. A further 15 had no visible windrows in the vicinity (within approximately 100 m radius) of the camera site. This is recorded as one of the on-site factors that may be of interest in influencing the target species, leading to detection at the camera site. Windrows composed of native logs, retained following the clearance of native vegetation to establish the plantation, generally included larger logs and logs with hollows, providing improving resource availability for both vertebrate and invertebrate classes (Brockerhoff et al., 2008, Thibault et al., 2016). Such hardwood windrows remain for decades while those comprised of the slash following plantation harvesting for re-planting, have smaller logs, few hollows and rot more rapidly.

3.2.2 Animal surveys

Fifteen of the 50 Reconyx HyperFire PC800 cameras deployed in the full survey of 150 sites (Chapter 2),

were deployed over three rounds to survey the plantation sites within each season (May to August 2014, henceforth “winter”, November to February 2014-2015, henceforth “summer”).

I recorded the UTM coordinates (GDA 1994 MGA Zone 55) of each camera site in the field using a GPS unit (Garmin GPSMap76CSX). The use of infra-red motion activated digital cameras provides a more robust estimation of the presence and abundance of cryptic species compared with data generated from live-trapping using cage traps or leghold traps, remote sampling of DNA and sand plots (Robley et al., 2010, Rowcliffe et al., 2008). Cameras are a simple and resource-effective method to utilise, are non-invasive and minimise site disturbance (Rowcliffe et al., 2008). Cameras were set for between 21 and 30 days to give a standardised minimum period of 21 days which is the recommended minimum deployment time to detect cryptic species such as cats and quolls if they are present in the landscape (Robley et al., 2010). The cameras were not revisited during that time Cameras were attached to trees at approximately 1.5m above the ground and aimed at the area of ground beneath lures that were suspended from an overhead branch 1.5 to 2m from the camera. Two types of lures were deployed at each camera: a bait lure and a CD to act as a visual lure. Lures increase the detectability of animals, which is useful when working with carnivores with very low detection probabilities (Robley et al., 2010). Lures can be food-based, phonic or visual (Robley et al., 2008). Food-based lures may contain a mix of ingredients to attract both predator and herbivorous prey species. Cats are visual predators relying on vision more than olfaction and a CD tied to a string and suspended from a branch so it can swing and rotate in the wind works as well as the white feathers used by Bengsen et al. (2011).

The bait lure consisted of a mixture of sardines and tuna oil to attract carnivores, and rolled oats and peanut butter to target herbivores. The placement of the lures 1.5m in front of the cameras and off the ground encouraged animals to stand up on their hind legs and allowed a good view of their undersides and backs. This increased the opportunity to identify individuals of all three carnivore species as they investigated the lures, by capturing a greater number of images at different angles (Hohnen et al., 2012, Saunders, 2012). A mixed carnivore and herbivore bait maximised the chance of attracting and detecting a range of species from both the predator and prey guilds (Reed, 2011). During winter, a shortage of tuna oil supply led to three different recipes being used, labelled B1, B2 and B3. To check whether the bait recipe had an effect on the results, it was included as a night-level factor in the analysis of detection probability.

Cameras were set on ‘rapidfire’ to record three consecutive shots with a less than one-second gap between, repeated while movement from an animal within range continued to be detected. This setting provided the best chance of identifying individuals of the three carnivore species because there

was a higher chance of capturing the animal's markings from different angles. For the winter round an oversight led to a number of cameras being set differently: 10 shots followed by a three second gap (1 camera) and 5shots/1sec (12 cameras). The difference in settings was included as a predictor variable for the detection model in the analyses as it could affect the number of images captured for each visit, and thus the chance of identifying individuals, although is not likely to have affected the likelihood of detection, or the presence/absence or abundance of the species at each site. Nightly or detection variables were recorded. These were variables that might change on each day or night during the time the cameras were set and might influence the probability of detecting a species on camera. They included: age of the bait lure, phase of the moon, recipe used for the bait (winter only), camera setting, camera round (cameras set over 3 rounds during each season) and co-presence of each of the predator species. A matrix was constructed for each of the detection variables to test for any influence at each site for the 21 days that the camera and bait were set. For example, the matrix for lure-age had values from 0 to 20 for each site as a count of number of nights the lure had been exposed to the elements, providing an indication of the influence of loss of scent of the lure on the mammals visiting the site. The eight moon phases recorded by the cameras were converted to four categorical variables in a matrix. Bait recipe and Round when the camera was set were treated in the same way. A matrix for the number of each of the carnivores detected on a nightly basis at each site was constructed and tested for influence of one carnivore on the detection of another.

3.2.3 Site variables

I recorded the following site-specific variables (Table 3-1): canopy height, shrub height, percent cover of canopy, percent cover of shrubs, visual occlusion at 25 cm and 50 cm above the ground, total stems of more than and less than 10 cm, presence and type of windrows. Windrows were scored as absent (NIL), or if present, composed of native vegetation (NAT) or clearfelled plantation timber (PL). Percent cover of the canopy and shrub layers were estimated using the projected foliage cover averaged over one hectare around the site (Michaels, 2006). Visual obstruction at 25 cm and 50 cm was measured using a 1 m x 1 m white sheet marked into 10 cm^2 grid squares, a variation on the "vegetation profile board" developed by Nudds (1977). The percentage of the sheet visible and not occluded by vegetation when held at 5m from the camera site was recorded with the observer squatting with their eye level at 25 cm and 50 cm, respectively. Four estimates were made, towards the north, east, south and west from the camera site, and a mean of the four values was used as a measure of line-of-sight visibility.

Table 3-1. Landscape and site factors selected for the estimated abundance modelling of spotted-tailed quolls, Tasmanian devils and cats in plantations in northwest Tasmania

Variable	Description	Mean, Range
Site level		
Canopy density	% canopy cover converted to proportion	0.36, 0.10 - 0.7
Shrub density	% shrub cover converted to proportion	0.25, 0.00 – 0.80
Visual obstruction at 25cm above ground	Converted % of sight sheet visible (N,E,S,W at 25cm), averaged	0.51, 0.06 – 0.98
Visual obstruction at 50cm above ground	Converted % of sight sheet visible (N,E,S,W at 50cm), averaged	0.57, 0.12 – 0.99
Total stems over ten 10cm	Stem density: Total number of stems N ,E, S, W >10cm	11.73, 2 – 28
Total stems under ten 10cm.	Stem density: Total number of small stems N ,E, S, W >2cm, <10cm	33.89, 0 – 170
Presence and type of windrows (nil/native/plantation)	Windrows presence and composition within 50m of site	Native = 21, Nil = 16, Plantation = 8
Landscape level		
Proportion of agricultural land within 1km radius	Desktop analysis proportion of ag land within 1km buffer	0.045, 0.00 – 0.43
Proportion of native forest land within 1km radius	Desktop analysis proportion of native forest within 1km buffer	0.29, 0.00 – 0.75
Tree age in 2014 derived from planting year	Plantation records: years to 2014 since establishment	11.38, 0.00 – 28.0
Plantation species (*Pinus radiata* or *Eucalyptus nitens)*	Plantation records	E.nitens 37, P.radiata 8
Plantation rotation (first, second or third)	Plantation records	1st = 16, 2nd = 27, 3rd = 3
Land use prior to planting (native forest/ agriculture)	Plantation records	Ag = 7, Nat = 38
Years since conversion (as at 2014)	Plantation records: years to 2014 since conversion from native forest or agriculture	27.8, 9 - 54

Physical obstruction was also measured to gauge whether there were differences in the way the predators moved through and around obstructing vegetation. This was done using a staff marked at 0-10cm, 10-30cm, 30-50cm and 50-100cm. The height division where vegetation touched the staff was recorded as a "1", division where no vegetation touched was recorded as "0". Physical obstruction was recorded at 1m intervals from 2 m to 5 m from the camera site in each of the four compass bearings (north, east, south and west) and a mean of these values used in analyses. Stem density was assessed by counting the number of stems between 2 cm and 10 cm in diameter, and also stems greater than 10cm, from the camera site (0 m) to 5m distance in each of the four compass bearings, with a mean of these values being used in analyses. Site-level variables measured at the camera site in the field were recorded on retrieval of the camera to minimise disturbance to the site, that could deter visits by the target species.

Plantation sites differed in the amount of structural complexity derived from the original land use, the species of tree planted, the density of planting and the age of the plantation. My aim was to sample even numbers of sites with more and less structural complexity. The difficulty of finding sites that satisfied a number of selection criteria however, meant the final sample included 21 sites with windrows composed of native timber logs, 8 with plantation timber and slash and a further 16 with no windrows visible near the camera site. Figure 3-2 & Figure 3-3 show a comparison between the understorey complexity between 1st rotation and 2nd rotation *E. nitens* plantations respectively.

Figure 3-2. E. nitens plantation, 1st rotation on converted native forest showing native log windrow and understorey regeneration

Figure 3-3. E. nitens plantation, young 2nd rotation crop, showing reduced understorey but remains of native windrows from the original native forest conversion

3.2.4 Landscape variables

Landscape-scale variables, such as the proportions of native forest and agricultural land within 1 km of the camera site, were obtained through calculations in ArcMap ArcGIS 9.3 (Table 3-1). Data on plantation ages, time since conversion, plantation species, previous land use and rotation number were sourced from Forestry Tasmania and Private Forests Tasmania (2016).

3.2.5 Data handling and analysis

Images were downloaded with the camera metadata (date, time, ambient temperature) and each animal recorded on camera was identified to species. Images of the same species separated by 5 minutes or more were considered to be separate records. Individuals of all three species of carnivores could be identified for each camera within each night using a combination of size and natural markings: devils from their white markings, quolls from their unique spot patterns, and cats from colour and the unique patterns of stripes on their front legs (where present). Where the same individual of one of these species returned to a camera on the same night it was counted as one detection only. All other species detected on the cameras were identified to species and the number of detections of each species each night on each camera was recorded. MapView Professional software was used to catalogue species detections at each site and image data were transferred into individual csv spreadsheets before combining into a master sheet of all site detections for that season.

Due to the risk of overfitting, predator and prey species abundance was not tested against the predator species except in a comparison of presence-absence with the raw data.

Data handling and analyses were conducted in R (Version 3.2), using the R-Studio (Version 0.99.896) interface and figures were created using the "ggplot2" package. I first constructed a Pearson's correlation matrix and selected just one of every pair of correlated variables, those with r values greater than 0.6. Variables were tested for normality and continuous site variables were then z-transformed so they were centred around zero, prior to occupancy modelling. Variables were back-transformed prior to making the final plots. No distance variables were used in the modelling.

Occupancy models were analysed using the "unmarked" package (Fiske and Chandler, 2011). Occupancy models have two parts. First, models with different combinations of the night or detection variables were tested and ranked. The detection variables in the final candidate set were then incorporated into all of the occupancy models. Secondly, occupancy is analysed in relation to factors that might influence the presence or abundance of a species at a site (site-level factors). Using prior knowledge of the biology and habits of the three target species, I constructed a plausible

set of hypotheses for landscape and site-specific factors that might influence the presence and population dynamics of the three carnivore species (Table 3-2). As I was able to individually identify carnivores detected on camera within each night, I used abundance – the actual counts of the number of unique individuals of each carnivore species recorded on each camera each night - as the response variable. This was implemented using the pcount function in “unmarked”.

In concordance with the 10:1 Rule of Thumb ratio for data to parameters, the number of variables tested in any one model was restricted to two, and the number of models tested for each species was restricted to five, to avoid over-fitting the models, given quolls and devils were recorded at just seventeen sites and cats at eleven sites during the winter survey. I tested only a few site variables thought to be relevant to the species use of plantations. The variables investigated for the plantation analysis are shown in (Table 3-1) rather than the full set that may influence carnivore use of the entire landscape (Chapter 2).

I used a multi-model inference approach, ranking the set of models using AIC values to determine the best explanatory variables as predictors of abundance of each of the carnivore species (Burnham and Anderson, 2002). Models within a Δ AIC of two of the top model (lowest AIC) were considered to have the strongest influence on the response variable. I determined the variables within these candidate models with an important influence on the response variable by the size of the effect (parameter estimate) and its standard error, as reflected in the p value in the model output table. To test the fit of the final model, I used a parametric bootstrap with a chi square test for binary data.

Table 3-2. Hypotheses and rationale used in the estimated abundance models to determine the influencing factors for spotted-tailed quoll, Tasmanian devil and cat abundance in plantations in northwest Tasmania

Hypothesis	Model script	Rationale
Spotted-tailed quolls:		
H1: quolls are present in higher abundance where the nitens plantation is on converted native forest	#M2 psi(orig_lu + spp1)p(varmoon)	Original landuse prior to conversion is a factor and quolls would prefer first rotation *E. nitens* plantations on converted native forest providing more diversity of understorey as habitat for prey
H2: quolls prefer older plantations on converted native forest	#M3 psi(zcon_age + zp_age)p(varmoon)	Older plantations provide more complexity in the understorey vegetation, with taller well-established native trees and shrubs providing diversity of habitat for prey
H3: presence of native log windrows and density of understorey influences use of plantations by quolls	#M4 psi(windrows + zvisob25)p(varmoon)	If they were using plantations for breeding , quolls would be more abundant in plantations with native log windrows and a dense understorey to assist in concealment of den sites
H4: windrows plus rotation number influences the presence of quolls	#M5 psi(rotation + windrows)p(varmoon)	Diversity of understorey would decrease in later plantation rotations so quolls were expected less often in second and third rotation plantations where the understorey would be impoverished
H5: windrows plus stem density (over 10cm dbh) influences the presence of quolls	#M6 psi(windrows + zstemoverten)p(varlure)	Quolls are expected to be more abundant where there is a higher number of trees providing habitat for prey and in conjunction with windrows, potential denning habitat
Tasmanian devil:		
H1: devils prefer older radiata plantations	#M2 psi(spp1 + zp_age)p(varlure + varmoon)	*P. radiata* is grown on a longer rotation so understorey trees and shrubs would be more mature but less dense than within *E. nitens* plantation
H2: devil presence influenced by understorey vegetation diversity found in plantations established on converted native forest and of greater age	#M3 psi(orig_lu + zcon_age)p(varlure + varmoon	Devils expected to be more abundant in older plantations established on native forest conversions as the understorey habitat would be similar to that found in native forests they prefer
H3: devils are more abundant where	#M4 psi(windrows + zvisob50)p(varlure +	Devils would be found where there is more structural complexity

windrows are present and there is more undergrowth reducing visibility	varmoon)	and density (lower visibility) in the understorey if they use plantations for breeding as windrows could provide denning sites
H4: Devil presence is influenced by the understorey complexity dictated by the time since conversion from native forest and whether 1st or 2nd rotation	#M5 psi(zcon_age + rotation)p(varlure + varmoon)	The time since conversion and whether 1st or 2nd rotation plantation influence the structural complexity and vegetation diversity of the understorey influencing prey availability and devil hunting success
Cat:		
H1: Cats prefer plantations near agricultural land and young plantations	#M2 psi(ag1k + zp_age)p(varmoon)	Cats are more common on the edges of agricultural land in a disturbed environment provided by young and newly established plantations that attract exotic prey species
H2 cats prefer nitens plantations established on agricultural land	#M3 psi(spp1 + orig_lu)p(varmoon)	Cats prefer more open country with less native vegetation understorey for hunting, which is found in plantations established on converted agricultural land. *E. nitens* is a more open plantation type compared with *P. radiata* which forms a dense canopy
H3: Cats prefer more open understorey for hunting success and will be less abundant where there are windrows and dense understorey (less visibility)	#M4 psi(windrows + visob25)p(varmoon)	While cats use vegetation for concealment to get close to hunting areas, they have more hunting success where it is more open with less opportunity for prey species to escape
H4: cat abundance is lower with increasing understorey complexity dictated by the time since conversion from native forest and whether 1st or 2nd rotation	#M5 psi(zcon_age + rotation)p(varmoon)	Cats are expected to be at higher abundance in plantations at a greater time since conversion and at second or third rotations, coinciding with lower understorey vegetation complexity

3.3 Results

3.3.1 Species recorded in each season

I recorded 21 species of mammals, 11 species of bird and 1 reptile at the camera sites in plantations. Quolls and devils were found in slightly more plantation sites than cats (quolls winter 36%, summer 38%; devils winter 44%, summer 38%; cats winter 29%, summer 24%)(Figure 3-4).

Within the critical weight range native prey group (native species <7000g, Tables 3.6 and 3.7), pademelons *Thylogale billardierii* were detected 10 times more often than brushtail possums *Trichosurus vulpecula*. Pademelons were detected at 93% of the sites in winter and at all sites in summer. Quolls, pademelons, possums, Bennett's wallabies *Macropus rufogriseus* and wombats *Vombatus ursinus* were detected at more sites in summer than in winter but the reverse was true for devils and cats. Within the large-prey group, Bennett's wallabies were more abundant in summer than winter while wombats were detected less often and differed little between winter and summer. Black rats *Rattus rattus*, were more numerous in winter than summer and made up a high proportion of the small and medium weight exotic prey species group. Also observed regularly were echidnas *Tachyglossus aculeatus*, southern brown bandicoot *Isoodon obesulus,* and long nosed potoroo *Potorous tridactylus.* Few rabbits were detected within plantations. The native bird, the Black currawong *Strepera fuliginosa,* was also detected regularly with more detections in summer than in winter. Full numbers of species detections are listed in the appendix (Table 3-6, Table 3-7,Table 3-8,Table 3-9).

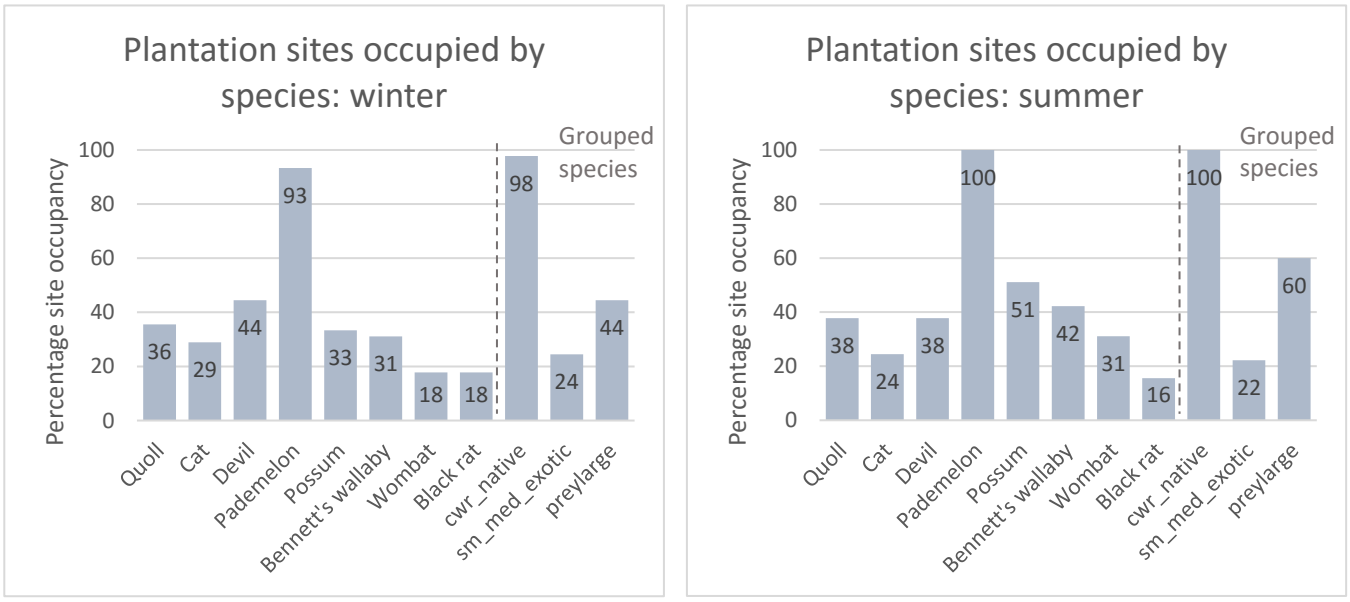

Figure 3-4. Comparison between winter and summer percentage of camera sites where each species of mammal and prey group was recorded in plantations in northwest Tasmania, Australia,.

3.3.2 Factors influencing occupancy and abundance of spotted tailed quolls

Variables influencing detection probabilities varied between winter and summer. The probability of detection of quolls was influenced by moon phase in winter and lure age in summer. These detection parameters were included in all occupancy models. The final candidate sets of models that describe factors influencing occupancy and abundance of quolls included two models with Δ AIC weight <2 in winter and one in summer. In winter more quolls were detected at sites with no windrows and had greater visibility at 25cm above the ground (quoll eye height), with a model weight of 55% (Table 3-3, Figure 3-5). The second model included rotation number of the plantation and windrows. There was higher estimated abundance of quolls in plantations with no windrows. This discounts my hypothesis (H3, Table 3-2) that presence of native log windrows and density of understorey influences use of plantations by quolls. My rationale was that if quolls were using plantations for breeding, they would be more abundant where there were windrows. The second best model, (H4, Table 3-2) indicated a weak influence on the abundance of quolls dependent on the plantation rotation, with a slightly greater abundance in first rotation plantations. The number of plantations in a third rotation were too few to model with confidence as indicated by the large standard error.

In summer, the top model had an AIC weight of 54%, suggesting quolls were again more likely to be detected and were more abundant at camera sites where no windrows were present and a greater number of stems over 10cm diameter (Table 3-3, Figure 3-6). The null model was the second top model with lure age as the detection factor, together suggesting a weak influence of windrows and stems over 10cm on the presence or abundance of quolls in plantations during summer.

Goodness of fit tests were run and these indicated a good fit of the models to the data for both winter and summer.

Table 3-3. Spotted-tailed quoll top models describing abundance and detection probability in plantations in north-west Tasmania in winter and in summer. Models within 2 of the lowest AIC (top model) were considered to have important influence on the abundance of the carnivore species, and only those parameters within these models that had a large effect relative to standard error are reported here. Parameter estimates relative to the intercept are reported with their standard errors. For categorical parameter estimates, the different levels of the parameter are listed, with the category represented as the intercept in brackets. Windrows categories: Nat = Native log windrows, Nil = none visible, Pl = Plantation slash windrows. Rotation categories: R1 = Rotation 1; R2 = Rotation 2; R3 = Rotation 3; Moon phase:FQ = 1st quarter, LQ+ Last quarter, NM= New moon, FM= Full moon

Model	AIC	ΔAIC	AICwt	Cumtv/ Wt	Occupancy - abundance (ψ)			Detection (p)	
Quoll									
Winter									
1	238.06	0.00	0.55	0.55	**Intercept** (Nat) -0.42 ± 0.65	**Windrows** (Nil) 1.28 ± 0.51 (Pl) 0.06 ± 0.82	**Visibility at 25cm** -0.32 ± 0.22	**Intercept** (FM) -2.84 ± 0.59	**Moon phase** (FQ) -1.65 ± 1.04 (LQ) -1.38 ± 0.48 (NM) -1.99 ± 0.63
2	239.21	1.15	0.31	0.86	**Intercept** -0.19 ± 0.64	**Windrows** (Nil) 1.62 ± 0.55 (Pl) 0.78 ± 0.9	**Rotation** (R2) -0.74 ± 0.49 (R3) -6.74 ± 34.11	**Intercept** (FM) -2.83 ± 0.57	**Moon phase** (FQ) -1.57 ± 1.04 (LQ) -1.36 ± 0.48 (NM) -1.98 ± 0.63
Summer									
1	266.90	0.00	0.54	0.54	**Intercept** (Nat) -0.40 ± 0.53	**Windrows** (Nil) 0.88 ± 0.47 (Pl) -0.18 ± 0.70	**Over 10cm stem density** 0.42 ± 0.17	**Intercept** -2.41 ± 0.52	**Lure age** -0.12 ± 0.03
2	268.75	1.86	0.21	0.75	-0.19 ± 0.37	Null		**Intercept** -2.13 ± 0.46	**Lure age** -0.12 ± 0.03

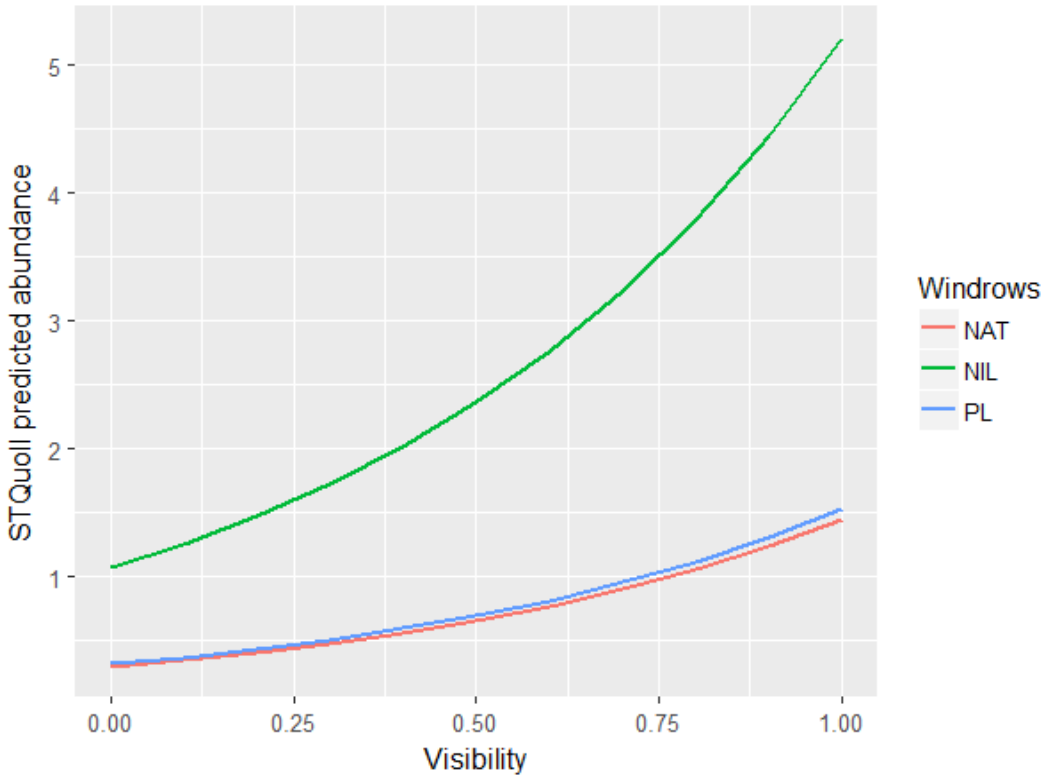

Figure 3-5 Winter predicted abundance of spotted-tailed quolls in plantations in northwest Tasmania with increasing visibility at 25cm height above the ground and the presence and type of windrows. Nat = Native log windrows, Nil = none visible, Pl = Plantation slash windrows.

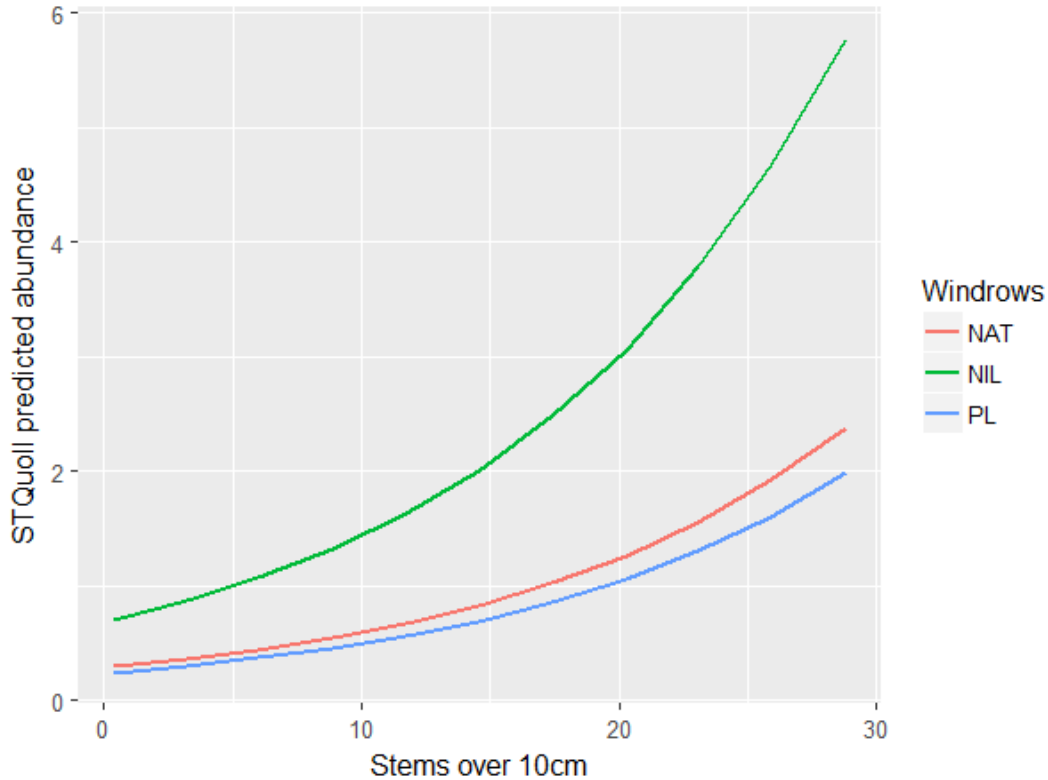

Figure 3-6. Summer predicted abundance of spotted-tailed quolls in plantations in northwest Tasmania with increasing number of stems over 10cm and the presence and type of windrows. Nat = Native log windrows, Nil = none visible, Pl = Plantation slash windrows.

3.3.3 Factors influencing detection, occupancy and abundance of Tasmanian devils

Factors varying each night of the survey influencing devil detection included bait recipe and moon phase in winter, and in summer the round when the camera site was surveyed. These night-level factors were included in all occupancy models.

There were three models with Δ AIC value <2 in the final set of candidate models for devils in both winter and summer. In winter (Table 3-4, Figure 3-7, Figure 3-8), devils had higher estimated abundance in plantations converted from original native forest rather than from agricultural land and in plantations with fewer years since the original conversion (34% model weight). In the second model, which had a weight of 26%, devils were more abundant in younger *E. nitens* plantations. The third model was the null model, suggesting the influence of the above factors was not strongly different from no influence. The top model supports H2 (Table 3-2) that devil presence is influenced by understorey vegetation diversity, found in plantations established on converted native forest and of greater age. The rationale being that devils were expected to be more abundant in older plantations established on native forest conversions, as the understorey habitat would be similar to that found in the native forests they prefer.

In summer the top model suggested support for H3: devils are more abundant where windrows are present and there is more undergrowth reducing visibility (Table 3-2). However rather than windrows of native logs, the top model included the presence of windrows comprised of plantation trees and less visibility at 50cm above ground (39% model weight) (Table 3-4, Figure 3-9). The second model (31% weight) included first-rotation plantations rather than subsequent rotations with fewer years since the original conversion to plantation (Figure 3-10). The third model indicated higher abundance of devils in older *P. radiata* plantations rather than in *E. nitens* (26% weight; accumulated AIC weight 96%) (Figure 3-11). Goodness of fit tests were run and these indicated a good fit of the models to the data for both winter and summer.

Table 3-4. Tasmanian devil top models describing predicted abundance and detection probability in plantations in north-west Tasmania in winter and in summer. Models within 2 of the lowest AIC (top model) were considered to have important influence on the abundance of the carnivore species, and only those parameters within these models that had a large effect relative to standard error are reported here. Parameter estimates relative to the intercept are reported with their standard errors. The different levels of the parameter are listed, with the categories represented in brackets. Occupancy categories: Original land use: Agricultural land = AL, Native forest = NF; Windrows categories: Nat = Native log windrows, Nil = none visible, Pl = Plantation slash windrows; Plantation rotation: Rt1= Rotation 1, Rt2 = Rotation 2, Rt3 = Rotation 3; Plantation species: Prad = P. radiata, Nit = E. nitens. Detection categories: Moon phase: FQ = 1st quarter, LQ= Last quarter, NM= New moon, FM= Full moon, Camera rounds (summer): Round1 = SR1, Round2 = SR2, Round3 = SR3; Bait recipe: B1 = Bait 1, B2 = Bait 2, B3 = Bait 3

Model	AIC	ΔAIC	AICwt	Cumtv/ Wt	Occupancy - abundance (ψ)			Detection (p)			
Devil											
Winter											
1	513.87	0.00	0.34	0.34	**Intercept** (AL) -1.15 ± 0.71	**Original landuse** (NF) 0.98 ± 0.73	**Conversion age (years)** -0.12 ± 0.21	**Intercept** (FM) -1.43 ± 0.27	**Lure age** -0.03 ± 0.05	**Moon phase** (FQ) -1.93 ± 1.21 (LQ) -0.12 ± 0.40 (NM) -0.94 ± 0.73	
2	514.43	0.56	0.26	0.60	**Intercept** (Nit) -0.17 ± 0.22	**Plantation species** (Prad) 0.88 ± 0.70	**Plantation age** -0.06 ± 0.19	**Intercept** (FM) -1.42 ± 0.27	**Lure age** -0.02 ± 0.05	**Moon phase** (FQ) -1.98 ± 1.22 (LQ) -0.14 ± 0.40 (NM) -0.99 ± 0.73	
3	515.53	1.66	0.15	0.74	-0.30 ± 0.22	Null		**Intercept** (B1)/(FM) -1.41 ± 0.26	**Bait recipe** (B2) -0.05 ± 0.37 (B3) 0.06 ± 0.71	**Moon phase** (FQ) -2.34 ± 1.04 (LQ) -0.33 ± 0.27 (NM) -1.34 ± 0.34	**Cat presence** -1.04 ± 1.07
Summer											
1	420.65	0.00	0.39	0.39	**Intercept** (Nat) -0.208 ± 0.357	**Windrows** (Nil) -0.18 ± 0.50 (PL) 1.22 ± 0.42	**Visibility at 50cm** -0.15±0.17	**Intercept** (SR1) -4.16 ± 0.57	**Round** (SR2) 2.19 ± 0.59 (SR3) 1.46 ± 0.60		
2	420.95	0.30	0.34	0.73	**Intercept** (Rt1) 1.02 ± 0.40	**Rotation No.** (Rt2) -1.39 ± 0.59 (Rt3) 10.98 ± 64.79	**Conversion age** (years) 0.78 ± 0.28	**Intercept** (SR1) -4.16 ± 0.57	**Round** (SR2) 2.19 ± 0.59 (SR3) 1.46 ± 0.60		
3	421.68	1.03	0.23	0.96	**Intercept** (Nit) -0.15 ± 0.26	**Plantation species** (Prad) 1.02 ± 0.44	**Plantation age** 0.21 ± 0.18	**Intercept** (SR1) -4.32 ± 0.58	**Round** (SR2) 2.38 ± 0.60 (SR3) 1.61 ± 0.60		

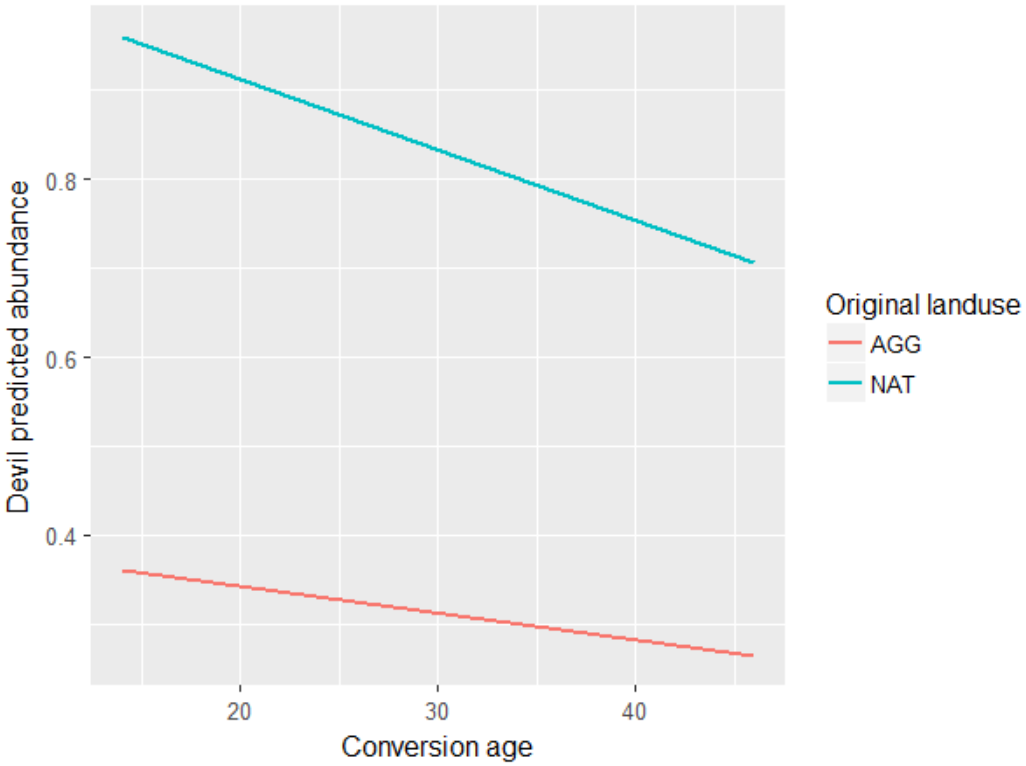

Figure 3-7. Winter predicted abundance of Tasmanian devils in plantations in northwest Tasmania from the top model, with increasing years since conversion and original landuse. AGG= Agricultural land conversion, NAT= Native forest conversion.

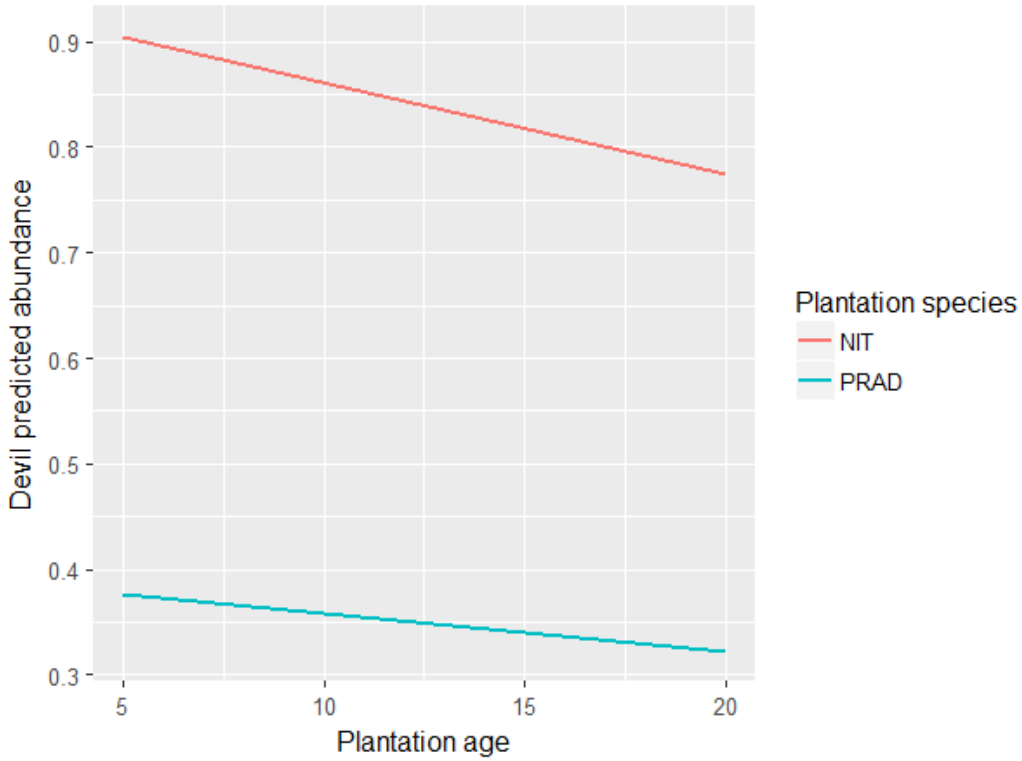

Figure 3-8. Winter predicted abundance of Tasmanian devil in plantations in northwest Tasmania from the second model, with increasing plantation age and plantation species. NIT= E. nitens, PRAD= Pinus radiata) plantations.

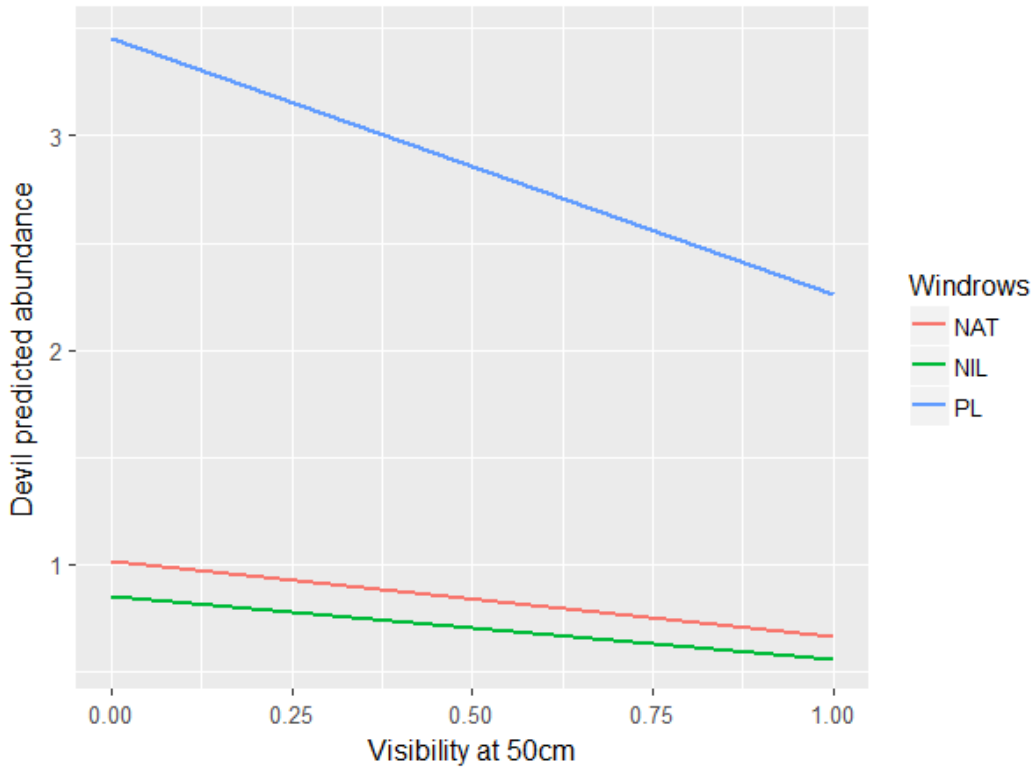

Figure 3-9. Summer predicted abundance of Tasmanian devils in plantations in northwest Tasmania from the top model, with increasing proportion of visibility at 50cm and presence and composition of windrows. Nat = Native log windrows, Nil = none visible, Pl = Plantation slash windrows.

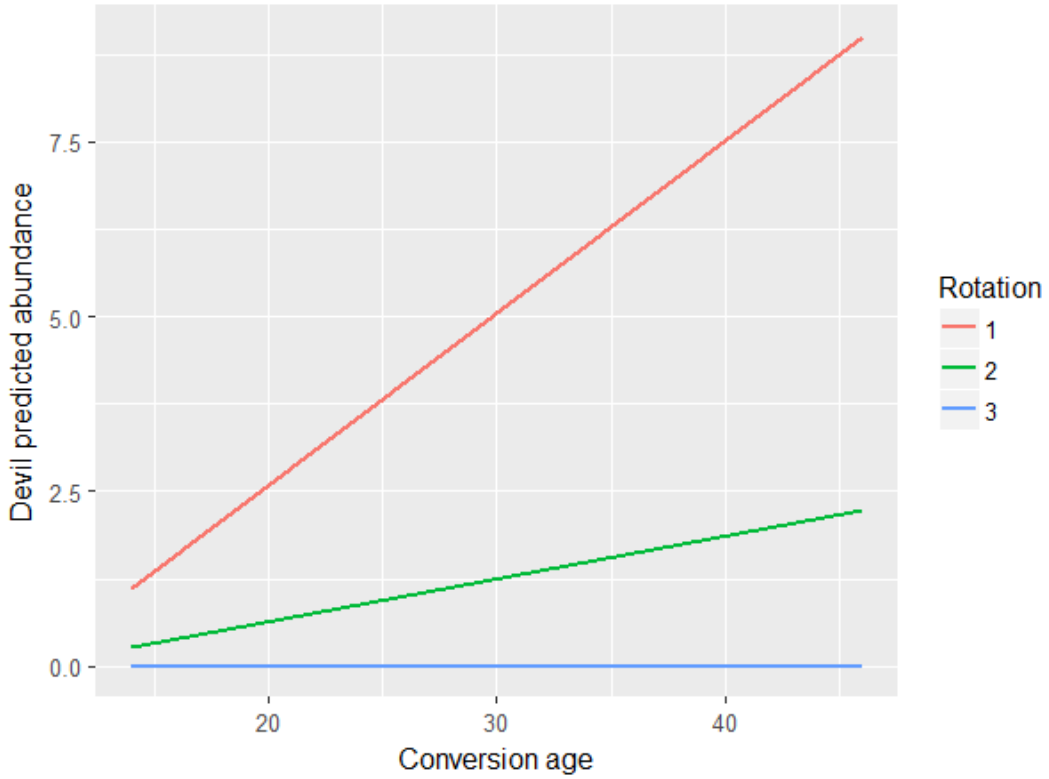

Figure 3-10. Summer predicted abundance of Tasmanian devils in plantations in northwest Tasmania, from the second top model, with increasing years since conversion and rotation number

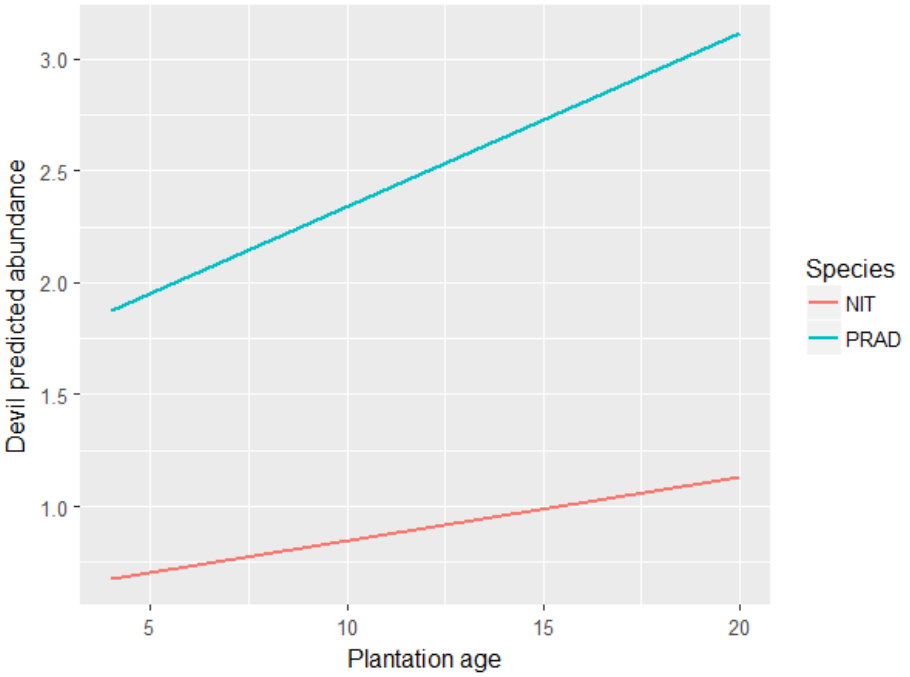

Figure 3-11. Summer estimated abundance of Tasmanian devils in plantations of increasing age from the third best model, against plantation species. NIT = E. nitens, PRAD= P. radiata

3.3.4 Factors influencing detection occupancy and abundance of cats

Moon phase, in particular increasing moonlight, negatively influenced the detection probability of cats in both winter and summer. This parameter was included in the detection model for all occupancy models.

For cats in winter, there was a single model with Δ AIC value <2 that described the factors influencing cat occupancy and abundance in plantations. In winter, cats were more abundant in younger plantations with a higher percentage of agricultural land within 1 km (Figure 3-12). This lends support to H1: Cats prefer plantations near agricultural land and young plantations (Table 3-2). My rationale for this was that cats would be more common on the edges of agricultural land in a disturbed environment provided by young and newly established plantations that attract exotic prey species. This model carried 66% of the model weight. The second model was the null model, which had a Δ AIC value of 2.84. While this model was just outside the rule of thumb cut-off of 2, it does indicate the result is not strongly different from the null.

In summer, the top model (Table 3-5, not plotted) was the null model (40% model weight), indicating no strong influences on cat abundance among those factors tested. The second-best model (not plotted) indicated the presence of a higher proportion of agricultural land within 1km of the site had a weak positive association with cat abundance while there is a weak positive association with pine plantations. Goodness of fit tests were run and these indicated a good fit of the models to the data for both winter and summer.

Table 3-5 Cat top models describing estimated abundance and detection probability in plantations in north-west Tasmania in winter and in summer. Models within 2 of the lowest AIC (top model) were considered to have important influence on abundance. Parameter estimates relative to the intercept are reported with their standard errors. The different levels of the parameter are listed, with the categories represented in brackets. Occupancy categories: Plantation species: Prad = P. radiata, Nit = E. nitens. Detection categories: Moon phase: FQ = 1st quarter, LQ= Last quarter, NM= New moon, FM= Full moon

Model	AIC	ΔAIC	AICwt	Cumtv/ Wt	Occupancy abundance (ψ) -			Detection (p)	
Cat									
Winter									
1	189.67	0.00	0.66	0.66	**Intercept** -0.46 ± 0.54	**Agriculture 1km** 0.20 ± 0.17	**Plantation age** -0.63 ± 0.30	**Intercept** (FM) -2.63 ± 0.59	**Moon phase** (FQ) -1.33 ± 1.06 (LQ) -2.93 ± 1.04 (NM) -1.01 ± 0.51
2	192.51	2.84	0.16	0.82	-0.56 ± 0.45	Null		**Intercept** (FM) -2.24 ± 0.53	**Moon phase** (FQ) -1.33 ± 1.06 (LQ -2.98 ± 1.04 (NM) -1.08 ± 0.51
Summer									
1	156.11	0.00	0.40	0.40	-0.16 ± 0.84	Null		**Intercept** -3.96 ± 0.88	
2	157.23	1.12	0.23	0.63	**Intercept** (Nit) -0.07 ± 0.72	**Agriculture 1km** 0.19 ± 0.23	**Plantation species** (Prad) 0.68 ± 0.73	Intercept -4.27 ± 0.72	Null

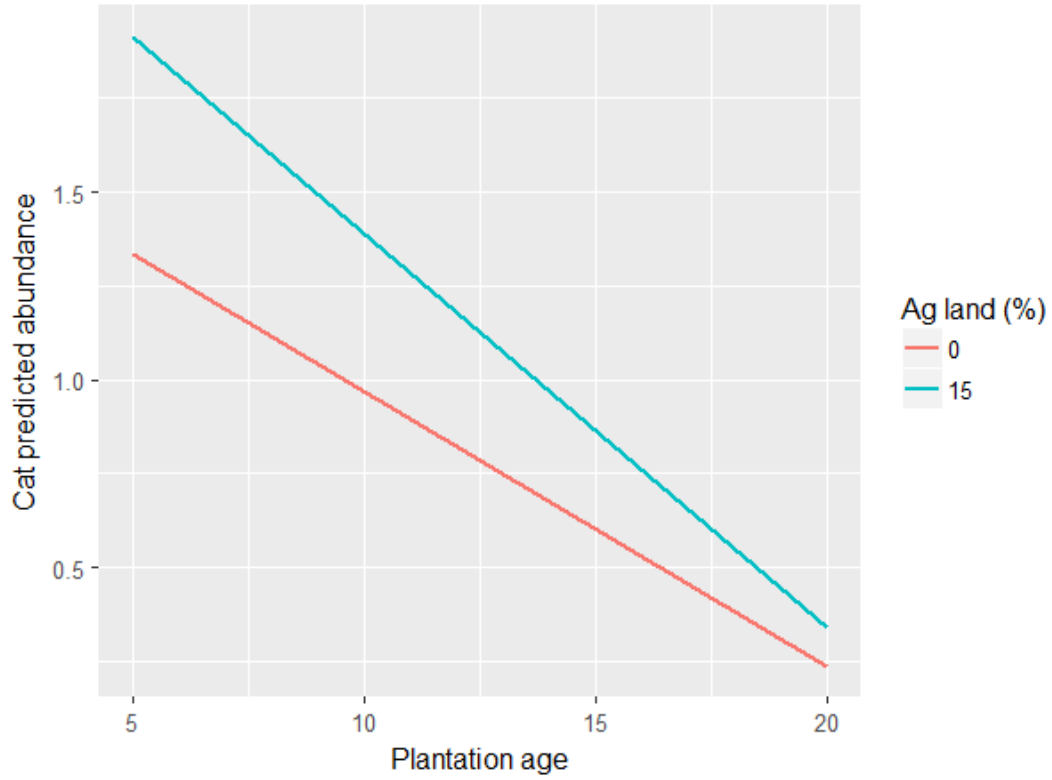

Figure 3-12. Winter estimated abundance of cats in plantations against plantation age (x-axis) and percentage of agricultural land within 1km (10th and 90th quantile) from the top model.

3.4 Discussion

The biodiversity of any plantation falls somewhere on the continuum between the simplified landscape of converted agricultural land and the more complex structure of a native forest conversion. This continuum is influenced by the time since conversion, presence and proximity of retained native vegetation and the complexity of the understorey, including large woody debris (Kavanagh et al., 2007, Grimbacher, 2011). Animal species diversity and plantation structure have been found to be directly correlated to the amount of native vegetation found within a plantation (Hartley, 2002). Within converted agricultural land more complex vegetation structure and enhanced connectivity between forest patches at a landscape scale, supports more prey and therefore predators (Bremer and Farley, 2010, Brockerhoff et al., 2008, Kanowski et al., 2005). However, plantations cannot fully replicate a natural forested community and will always be missing elements found in a native forest, whether they be plant or fauna species, woody debris or complexity within the forest structure. This will influence the animal species that can inhabit the plantations either permanently or transiently.

The results of this study provide new insights into the factors associated with the detection and abundance of the three target species within plantations. Such information may be used to inform management of plantations where enhancing the value of the area for the threatened quoll and devil is a management objective. Seasonal differences were also evident for all species in their associations with different elements of plantations. The three species varied in their association with different types of plantation, different structural elements and between the summer and winter seasons. In contrast to devils and cats, quolls were more abundant at more plantation sites in summer than in winter. Quolls had little association with windrows within plantations in both seasons. In winter quolls were in higher abundance where there was greater visibility, and in summer, where there was a greater number of trees. Devils were more abundant in plantations during winter and were found more often in younger *E. nitens* plantations established by conversion of native forest rather than of agricultural land. In summer devils were more abundant where there was more undergrowth, where there were windrows comprised of the slash from harvesting of plantation trees and in older first rotation *P. radiata* plantations. Cats appeared to make little use of plantations and no site-specific attributes were strongly associated with cat abundance in plantations. The main association of cats with plantations was their presence in young plantations within 1km of agricultural land where cats were common (see Chapter 2).

While the total number of detections of the three species varied between seasons, the overall patterns of occupancy and abundance were consistent, indicating the methods for attracting and capturing images of the three species was successful in gaining a representative sample of the populations in plantations. The strength of association of all three carnivores with plantation attributes were weaker than for the larger study encompassing native forest and agriculture as well as plantations. This may be a result of the smaller sample size in the survey of plantations and low numbers of the target species in plantations, or the tested attributes of plantations may simply have little effect on use by carnivores. The results indicate each species must be considered separately regarding their use of plantations, taking into account their breeding seasons and requirements, prey preferences and availability, and mode of hunting.

3.4.1 Spotted-tailed quolls

That quolls were not associated with windrows in plantations in winter suggests plantations possibly do not provide either suitable denning sites or sufficient prey to support breeding females and this may restrict the use of plantations by quolls. This challenges my hypothesis that quolls would be found in higher numbers in plantations containing windrows because these features may provide

den sites and potentially also concealment for hunting. If quolls were using plantations for breeding, windrows would be the obvious choice for den sites. Breeding occurs in winter, with mating from late June to early August, birth of young in July/August, and weaning in December so females would be reliant on consistent maternal den sites probably from June to December (Belcher, 2004, Jones and Barmuta, 1998, Jones et al., 2001).

Quolls use a variety of den sites, including under large rocks, hollow logs and trees, windrows and small wombat burrows, and individual quolls may use more than 15 den sites at any time (Belcher and Darrant, 2006). Dens are consistently cryptic, with entrances typically hidden by vegetation or rock overhangs. It is unlikely plantations (apart from those established in karst areas) would provide sufficient suitable den sites and prey to support a breeding female, particularly those established on previously cleared farmland.

The low use of plantations by quolls may also reflect a low diversity of preferred prey in plantations. The diversity of animals in monoculture plantations established on agricultural land is lower than those established on converted native forest (Grimbacher, 2011, Brockerhoff et al., 2008). In turn, plantations established following native forest conversion are lower in biodiversity compared with the original native forest (Kanowski et al., 2005, Lindenmayer and Hobbs, 2004, Carnus et al., 2006). The diet of quolls is composed of small to medium animals (500-7000g) with a greater proportion of invertebrates and reptiles in summer, and a shift towards more mammals in winter (Glen and Dickman, 2006a). Larger male quolls concentrate on medium to large mammal prey, while the major dietary component for females and juvenile males is small mammals and birds (Jones and Barmuta, 1998). Although the number of detections of each of the prey species was not tested in the models for plantations in this study, the presence and total activity of critical weight range mammalian prey are found to positively influence quoll abundance (Chapter 2). This interpretation is further supported by the association between quolls and high line-of-sight visibility (or low visual occlusion) of the places quolls were found. Very open plantation forests are unlikely to provide suitable habitat for the major prey species of quolls.

Most of the quolls detected were likely to be adult males transiting through the plantation between more suitable habitats or young males using suboptimal habitat. This interpretation is supported by the results of another study of quolls undertaken in northwest Tasmania in 2002-2003. Hawkins and Jones (2003) found a highly skewed sex and age ratio for quolls in production forest. Of a total of 22 quolls trapped in a 12-month period, 20 were adult males and the two females were both non-breeding sub-adults (Hawkins and Jones, 2003). Troy (2014) found quolls to have a strong preference for native eucalypt forest and suggested males, being more mobile than females, would be able to

travel through less suitable habitats in search of females and prey.

3.4.2 Tasmanian devils

Devils use plantations more than quolls and were found in plantations with windrows comprised of plantation slash in summer, although not in winter. Devils are more abundant in younger *E. nitens* plantations on land converted from native forest. Such plantations have plentiful regeneration of native shrubs and trees between the plantation trees in the early stages of plantation establishment, providing browsing and shelter for native herbivores. This more varied and complex understorey may support more prey. This aligns with the dietary preferences of devils during winter, i.e. medium sized animals such as the pademelon *Thylogale billardierii* (Jones and Barmuta, 1998) which prefer more undergrowth for refuge. The seemingly opposing use of older *P. radiata* forest is likely to be due to a longer growing period for pines for sawlog (as opposed to eucalypts grown for pulp on a short rotation), resulting in more mature native understorey vegetation and open clearings interspersed within the pines, and an overall less disturbed environment. A probable reason is that devils consume a greater number of large prey than quolls (Andersen et al., 2016) and this difference is strengthened over summer with a shift towards larger prey species such as wombats *Vombatus ursinus* and Bennett's wallabies *Macropus rufogriseus* (Jones and Barmuta, 1998). These species are found in more open forests, including plantations with a grassy understorey, such as *Poa labillardierei* tussock country.

Female devils may use the plantation slash windrows as maternal dens during the summer. Young devils emerge from the pouch and are deposited in a den in August and use the den until they are weaned in early February (Guiler, 1970, Jones and Barmuta, 1998). However, there is only weak support for the use of windrows by devils in summer.

3.4.3 Cats

Cats were more abundant in winter in younger plantations and in proximity to a greater proportion of agricultural land within a 1km radius of the camera site. This aligns with their use of edges of agricultural land, likely to provide greater hunting opportunities and prey (Chapter 2). My "winter" season ran from May to August and includes the peak rabbit breeding season in late winter/early spring (Catling, 1988). Studies in mainland Australia have shown that in open or disturbed habitats cats favour rabbits as their staple diet during this period, corresponding with cat breeding season (Catling, 1988, Coman and Brunner, 1972). In more intact native habitat, cats target smaller native mammals, reptiles, invertebrates (Coman and Brunner, 1972, Kutt, 2012). The younger plantations, prior to the growth of the understorey, retain some of the features of agricultural land and would

probably be used for hunting. My larger multi-use landscape study (Chapter 2) suggests cats may target rabbits on farm-edges and/or other small to medium size prey elsewhere. Fewer cats inhabited plantations with only 29% and 24% of plantation sites with occupancy in winter and summer, respectively. This is probably a result of few rabbits, their favoured prey species, inhabiting plantations.

3.5 Conclusion

The larger of the marsupial carnivores, the Tasmanian devils and spotted-tailed quolls, use plantations but are more abundant in nearby native forests. When they are in plantations they respond to different elements of the habitat. Quolls more commonly occur in open plantations, indicating they are more likely to be transiting through them. Devils appear to prefer dense understorey in plantations during winter and more open plantations in summer. Their greater abundance in plantations with windrows suggests possible use of windrows for denning. Cats mainly occupy the plantations close to agricultural land. Maintaining a dense understorey for the life of the plantation may deter cats from using plantations, however young plantations are synonymous with disturbance, and this appears to attract cats.

Quolls may make limited use of plantations, likely because plantations do not provide the food and denning resources they need. To encourage use of and breeding in proximity to plantations by quolls and devils, structural elements could be installed for use as denning sites. These could be placed on the edges of the plantations, within streamside reserves, and in parts of the landscape with lower production values, such as rocky areas excluded from planting. This management action could be implemented rapidly. Longer term management actions for both quolls and devils could be directed at maintaining or encouraging vegetation diversity within the plantations through both mixed plantings and encouraging understorey species to benefit animal diversity. Mature plantation trees are of a relatively young age compared to native forest and hollows are not naturally available. Artificial hollows can be installed to increase the use of plantations by hollow dependent species (Goldingay et al., 2015). There is the potential to introduce more structural complexity into the forest as it grows (Carnus et al., 2006, Lindenmayer and Hobbs, 2004). To provide connectivity and diversity within the landscape, strategies could include: retaining existing areas of remnant native vegetation within plantation stands and replanting native vegetation corridors (Munks and McArthur, 2000), promoting a native vegetation understorey, and undertaking mixed plantings with a mosaic of differing growth habits and ages for harvest. Retaining plantation slash provides the

conditions to support fungi and invertebrates, in turn feeding birds and small mammals. These measures would benefit all trophic levels (Deal et al., 2017, Taylor et al., 2007, Lindenmayer et al., 2000), including the marsupial carnivores that may benefit from the capacity of these more diverse plantations to exclude cats (Hollings et al., 2013a).

This study raises further questions for research. I used broad categories for the composition of the windrows and there could well have been a mix of plantation and native logs in some windrows. The size of logs and the presence of hollows and potential burrows under the windrows likely influences their potential use by quolls and devils as denning sites. This would vary between windrows comprised of native or plantation slash logs. In addition, some of the plantations I recorded as having no windrows may have had potential denning sites including windrows nearby, not visible from within the camera site area. A more thorough investigation of potential den sites in plantations would be of value as well as a direct comparison with potential den sites in adjacent native forest. Further research of the abundance of prey species and the diet of quolls and devils in plantations in different seasons and at different stages of the breeding cycle would enhance understanding of the value of plantations for quolls and devils at different times of the year. Trapping surveys in a capture—recapture framework could provide insights into the demography of quoll and devil populations in plantations, including age structure, sex ratio and whether individuals are permanent residents or transient. Tracking using GPS collars would allow measurement of movement patterns and fine-scale habitat use, to determine whether quolls and devils utilise plantations for denning, predation or merely a component within their hunting range.

Plantations can be managed for biodiversity. There are examples worldwide where modification in plantation design and management to increase structural complexity in plantations has led to higher diversity outcomes. This involves consideration of multispecies plantings, longer rotations, managing at a landscape scale, retaining more large woody debris and consideration for connectivity in the landscape, including retaining areas of native vegetation to provide suitable habitat (Brockerhoff et al., 2008, Carnus et al., 2006). Further research into methods to enhance vegetation diversity and structural complexity in areas important for the marsupial carnivores, whilst also meeting the primary wood production aim of plantations in Tasmania, would have universal applications for plantation management.

3.6 Appendix - plantations

Table 3-6. Detections of small prey species <500g by season in plantations used in the grouping which included both native and exotic species, "cwrnative" which includes small and medium native prey species, and "sm_med_exotic" which is a count of small and medium weight exotic species detections

Species	Common name	Avwt (g)	Native/exotic	Wint PL	Summ PL
Anthochaera paradoxa	Yellow wattlebird	*175*	*Native*	*0*	*5*
Cercartetus nanus	Eastern pigmy possum	*24*	*Native*	*0*	*1*
Mus musculus	House mouse	*15*	*Exotic*	*2*	*0*
Phaps chalcoptera	Common bronzewing	*317*	*Native*	*0*	*1*
Phaps elegans	Brush bronzewing	*200*	*Native*	*0*	*3*
Platycerus caledonicus	Green rosella	*140*	*Native*	*0*	*1*
Pseudomys higginsi	Long-tailed mouse	*67*	*Native*	*0*	*3*
Rattus lutreolus	Swamp rat	*122*	*Native*	*3*	*0*
Rattus rattus	Black rat	*280*	*Exotic*	*75*	*27*
Sericornis frontalis	White-browed scrubwren	*12*	*Native*	*0*	*2*
Sericornis humilis	Tasmanian Scrubwren	*18*	*Native*	*1*	*0*
Small animal			*Native*	*0*	*1*
Strepera fuliginosa	Black currawong	*374*	*Native*	*16*	*57*
Tiliqua nigrolutea	Blotched bluetongue	*500*	*Native*	*0*	*1*
Turdus merula	Blackbird	*89*	*Exotic*	*0*	*1*
Zoothera lunulata	Bassian thrush	*100*	*Native*	*10*	*7*
Grand total:				*107*	*110*

Table 3-7. Detections of medium prey species >500g and 7000g by season in plantations used in the "cwrnative" grouping which includes small and medium native prey species, and "sm_med_exotic" which is a count of small and medium weight exotic species detections

Species	Common name	Avwt(g)	Native/exotic	Wint PL	Summ PL
Corvus tasmanicus	Forest raven	650	Native	*1*	*3*
Isoodon obesulus	Southern brown bandicoot	775	Native	*26*	*10*
Medium animal			Native	*6*	*18*
Oryctolagus cuniculus	European rabbit	1580	Exotic	*2*	*3*
Perameles gunnii	Eastern barred bandicoot	640	Native	*0*	*2*
Potorous tridactylus	Long-nosed potoroo	1100	Native	*43*	*76*
Pseudocheirus peregrinus	Common ringtailed possum	900	Native	*0*	*2*
Tachyglossus aculeatus	Echidna	4500	Native	*19*	*55*
Thylogale billardierii	Tasmanian pademelon	5450	Native	*714*	*1310*
Trichosurus vulpecula	Common brushtail possum	2875	Native	*71*	*148*
Grand total				*882*	1627

Table 3-8. Detections of large prey species > 7000g by season in plantations. Only native species detected in plantations to be included in the "preylg" grouping for analysis

Species	***Common name***	***Avwt(g)***	***Native/exotic***	***Wint PL***	**Summ PL**
Macropus rufogriseus	Bennett's wallaby	16850	Native	52	222
Vombatus ursinus	Common wombat	26000	Native	23	28
Grand total				75	250

Table 3-9. Detections of all predator in plantations species by season.

Species	***Common name***	***Avwt (g)***	***Size class***	***Native/ exotic***	***Wint PL***	***Summ PL***
Accipiter novaehollandiae	Grey goshawk - white phase	545	med	Native		1
Canis lupus familiaris	Domestic dog	16000	large	Exotic		1
Dasyurus maculatus maculatus	Spotted-tailed quoll	5500	med	Native	35	43
Dasyurus viverrinus	Eastern quoll	1090	med	Native	3	5
Felis catus	Cat (feral & domestic)	4050	med	Exotic	22	16
Sarcophilus harrisii	Tasmanian devil	7000	large	Native	89	77
Sminthopsis leucopus	White-footed dunnart	23	small	Native		1
Grand Total				**Totals**	149	144

Chapter 4 General Discussion

This study assessed the influences of habitat and land use on the abundance of three mammalian predators, the native spotted-tailed quoll and Tasmanian devil, and the invasive cat in a modified landscape in northwest Tasmania, Australia. The four land uses tested during this study were native forest, agricultural land, native grasslands/moorlands and plantations. I sought to determine the key landscape factors influencing where each of the three species is found, the structural components at a site level influencing their abundance, and whether there were differences in landscape use by each predator species with respect to the other two. I examined the data from a subset of the camera sites in more depth to understand the factors influencing the use of plantations by quolls, devils and cats. In this chapter, I will synthesise my findings and discuss their implications for management of habitat to encourage the native predators and discourage cats. I will identify the gaps in knowledge where more research is required to understand the factors influencing the abundance and distribution of the three predators.

4.1 Key results

Quolls and devils overlap generally in their use of this modified landscape, but there are differences in the factors influencing their occupancy and abundance at particular sites. In contrast, although they occur over the entire study area, cats are most abundant in proximity to and on the margins of agricultural land. Season appears to influence patterns of occupancy and abundance for predator and prey species.

The results suggest occupancy and abundance of quolls is strongly influenced by habitat factors including presence of tall forests, dense understorey and preferred prey species. Among sites in plantations, quolls were more abundant in open plantations with no windrows. This suggests plantations do not provide the resources required to sustain resident breeding populations of quolls and those quolls detected in plantations may have been travelling through them rather than permanently occupying them. As the quolls seek cryptic den sites (Belcher and Darrant, 2006) for breeding and raising young, there should have been some indication of selection for sites providing denning opportunities. Plantations with a higher density of understorey and presence of windrows should have had a higher abundance of quolls if they were using den sites in plantations. Quolls using plantations are most likely to be predominantly males outside the mating season or subadults dispersing from their natal range. Male quolls have larger home ranges than females and neither the sub-adult or male population class has to service the high energy demands of rearing young.

Devils are more abundant in native forest at higher elevation where there are also more wombats, although devils are also present in lower numbers in plantations and at the interface with agricultural land. Use of plantations by devils changes with season, from younger eucalypt plantations in winter to older pine plantations in summer. These differences may be associated with seasonally varying requirements for food and shelter at different stages of the annual breeding cycle (Friend, 1980, Jones and Barmuta, 1998).

Cats are found throughout the study area but are in higher abundance in proximity to and on the margins of farmland. In the winter cats are in greater abundance in younger plantations close to agricultural land (Chapter 2, Figure 2-16) while in summer there are no strong plantation factors influencing cat abundance. There is a positive association between abundance of quolls and devils. Other studies have identified differences in diet of the two species that may result in a degree of niche partitioning within their shared habitats (Jones and Barmuta, 1998). There is no discernible positive or negative association during winter between cats, quolls and devils, however in summer cats were positively associated with devils and negatively with quolls.

4.2 Responses of native and alien carnivores to modified landscapes

The results of the study are broadly consistent with other studies, which also find devils and quolls both prefer structurally complex forest habitat but will use fragmented landscapes, particularly where there is good connectivity between the forest patches (Troy, 2014, Andersen, 2016, Saunders, 2012, Belcher and Darrant, 2004, Glen and Dickman, 2011). Plantations, being simplified versions of the natural forested environment, allow examination of a subset of the variables influencing the use of the landscape by these species. In Tasmania plantations are monocultures. Most comprise *Eucalyptus nitens* but some are planted with *Pinus radiata.* The plantation species, age of the plantation and whether it was established on agricultural land or land converted directly from native forest, influences the diversity of the understorey (Hartley, 2002, Bonham et al., 2002). The patterns of use by the three predators illustrate the differences between the three species in the wider landscape and in plantations.

None of the carnivore species made extensive use of plantations. The quoll, the more specialised arboreal predator, was more restricted than devils and cats to areas providing the structural complexity required for multiple den sites and opportunities to hunt arboreal prey. Other studies on medium-sized and small predators have also found varying degrees of tolerance to habitat disturbance. Some predator species will use fragmented landscapes for hunting but need a core area of structurally complex mature forest to supply their fundamental niche requirements (Hearn et al.,

2010). Native predators are more abundant and species-rich in contiguous rather than fragmented forests, whether it is martens in western Quebec, pine martens in Scotland or predatory species in the rainforests of Madagascar (Potvin et al., 2000, Caryl et al., 2012). Den sites and primary prey were found to be limited in intensively managed plantation forests (Caryl et al., 2012). As with the devils, quolls and cats, the Malagasy civet *Fossa fossana* and the fossa *Cryptoprocta ferox* showed differing responses to intact native forests, timber harvesting and fragmentation. The Malagasy civet was not found in fragmented rainforests and used selectively logged forests at reduced densities, preferring intact rainforest, while the fossa occupied forest, selectively logged areas and forest fragments close to (2.5km) large areas of continuous forest, but was absent from fragments more distant from its core habitat (Gerber et al., 2012).

Quolls are specialised hunters well adapted for climbing. They spend more time above ground than either devils or cats, moving along fallen logs and in trees, where they also hunt for prey (Andersen, 2016, Jones and Barmuta, 2000, Glen and Dickman, 2006b). Native forest typically has a wide range of plant species and tree ages, including senescent trees that provide hollows for denning by quoll as well as hollow-dependent prey species. Quolls have home ranges of approximately 528ha (Andersen, 2016) and because they depend on native forests to supply both prey species and den sites, their occupancy of native forests, where forests occur at large extent and in good condition, is generally high (Glen and Dickman, 2011). Increased activity of this species during the winter coincides with the breeding season. Females typically use non-overlapping home ranges (except for mothers and daughters, who may have shared ranges) (Troy, 2014, Firestone et al., 1999, Glen and Dickman, 2006b) where individual female quolls move their litters regularly between dens (Glen and Dickman, 2006b). Agricultural land would have limited capacity to support breeding females with the energy (food resources) and denning requirements needed to raise young. Troy (2014) found, as with this study, that quolls primarily occupy native forest. Where native forest is highly fragmented in agricultural landscapes, quolls have larger home ranges in total, although the total amount of forest contained within the home ranges of individuals living in more and less fragmented areas is similar (Troy, 2014). These factors may account for the reduced abundance of quolls in agricultural areas.

Dependence on specific habitat for reproduction is recorded in other specialist predators such as fishers *Martes pennanti* in British Columbia, Canada. Female fishers select forests with larger diameter trees, more likely to have the hollows that females require for denning (Weir et al., 2012). Other studies indicate sensitivity of small to medium-sized predators such as martens, Iberian lynx and genets, to the availability of denning sites used for shelter, protection from predation and raising young, that are provided by older and more structurally complex forests (Potvin et al., 2000,

Carvalho et al., 2014, Fernández and Palomares, 2000). In a disturbed landscape, species that use multiple den sites, such as quolls *Dasyurus maculatus*, genets *Genetta genetta*, eastern spotted skunks *Spilogale putorius* and raccoons *Procyon lotor*, are potentially limited in reproductive capacity by the availability of den-sites (Fernández and Palomares, 2000, Lesmeister et al., 2008, Glen and Dickman, 2006b, Beasley and Rhodes, 2012). Monoculture plantations, as with grasslands and agricultural land, have a simplified structure, lacking diversity of plant species and form, understorey and availability of hollow trees. Plantation trees provide few if any hollows. A study of quolls in far northwest Tasmania found they may be abundant in a fragmented landscape where patches of native vegetation are connected by features providing cover that allow them to transit between patches. Here they have access to abundant populations of prey on or adjacent to productive farmland, with a high degree of edges between pasture and forest fragments (Troy 2014). Rather than typical den sites, in this case quolls used resting sites in patches of tall grass and small copses of native or exotic vegetation in otherwise open country (Troy, 2014, Saunders, 2012, Andersen, 2016). Use of maternal den-sites in this landscape remains to be investigated.

The devil was the most abundant of the three predator species across all habitat types, including plantations. Devils have home ranges which, at around 1300 ha, are significantly larger than those of quolls, and have a generalised diet which includes a high proportion of material obtained by opportunistic scavenging (Pemberton et al., 2008). These two factors suggest that devils are more flexible in their habitat preferences than either quolls or cats. Nonetheless, devils are more abundant in structurally complex habitats, as shown by the results of the full study (Chapter 2) and the plantation study (Chapter 3). This is consistent with their pounce-pursuit style of hunting (Jones, 2003) where they use cover to get close to prey. Devils also prefer structures such as burrows or caves for denning, but do not appear to be restricted to using dens in native forest. For example they are occasionally recorded denning and raising young under houses and sheds (Mounster, 2017, Parer and Parer-Smith, 2003). While male devils may use several dens, females use a single maternal den, in contrast to several required by quolls (Pemberton, 1990). In addition, the high abundance of prey on the interface between native forest and agricultural land suggests devils may not be limited by prey availability in partially fragmented landscapes.

There are a number of possible explanations for the positive association between devil and wombat detections and abundance at higher elevation, including a possible higher reliance on wombats either as a prey species or by providing an abundance of large burrows for den sites (Andersen, 2016). The contribution of wombats to the diet of devils varies substantially with location (Andersen, 2016, Pemberton et al., 2008, Jones and Barmuta, 1998). Neither prey availability nor habitat, appear to be limiting devil abundance. In this study, the gradient in the distribution and abundance

of devils may reflect the timing of the local outbreak of DFTD as it spread from east to west. This would exemplify the danger of drawing conclusions from what may in fact be a coincidental association with wombat abundance. Another hypothesis is that there is a relationship between abundance and productivity related to rainfall, creating a positive gradient east to west and consequently higher prey availability further west (Andersen, 2016). This would be an example of an indirectly related association with wombat abundance. Devils occupy a generalist predator role and the reduction of abundance of devils is likely to have had repercussions on their prey species. Until 1946, devils were considered rare in Tasmania and confined to the more rugged areas of the State (Guiler, 1970). Between 1946 and 1960 the population appears to have increased, and devils to have become more widespread, following the extinction of the Thylacine (Guiler, 1970). A considerable population increase in native herbivores has also occurred because of pasture improvement and increased forest fragmentation, combined with the recent losses of up to 95% of the devil population in some areas (Hollings et al., 2013a, Norton et al., 2010). This effect is echoed in the increase in wallaby populations in Booderee National Park (BNP), in south-eastern Australia. Here the population increased sharply following removal of alien predators and in the absence of any native predators. This has resulted in over-browsing of native vegetation and changes to vegetation recruitment and composition (Dexter et al., 2015).

Globally other herbivore species have shown changes in population following a reduction in predator populations. The increase in elk in Yellowstone National Park following extirpation of wolves and prior to their reintroduction is an example (Ripple and Beschta, 2003). Eagan et al. (2011) found populations of white-footed mice increased where raccoon abundance was reduced, while Terborgh et al. (2001) found the absence of top-down control from predators had strongly detrimental effects on vegetation due to uncontrolled browsing by herbivore populations on predator-free islands. In the absence of the thylacine in Tasmania, the devil is the top predator and maintaining their population in the face of the DFTD is important to retain some top-down pressure on the native herbivores.

Studies of cats in many countries have found them to be highly adaptable to a wide range of habitat types, although their spread is often assisted by human disturbance such as degradation and fragmentation of native habitat. Globally cats have widespread and detrimental impacts on native wildlife (Farris et al., 2017, Doherty, 2014, Harper, 2007, Goltz et al., 2008). Cats are more abundant in open, disturbed landscapes, which provide them with greater hunting success, but they too prefer habitat complexity, probably associated with availability of shelter and cover for movement through the landscape (Hohnen et al., 2016, Hollings et al., 2013b, McGregor et al., 2015). Although cats were distributed over the entire study area, they were most abundant in proximity to and on the

margins of farmland, and were also moderately abundant in native forest. Their abundance in native forest may be related to the presence of prey, but is also likely to be supported by the availability of shelter and den sites (Harper, 2007). A fragmented interface between agricultural land and bushland containing large trees provides cats with cover for refuge as well as hunting. Cats favour more open areas for successful hunting (Hohnen et al., 2016, McGregor et al., 2015, McGregor et al., 2016) but preferentially use dense shrubbery for cover at the interface between the paddocks and forests for movement (Bengsen et al., 2012, Edwards et al., 2002). Areas of remnant forest on the edges of or interspersed with pasture, can be found on most farms in the study region, providing potential den sites for cats. This enables cats to hunt within the plantations and return to shelter in the forested remnants in nearby agricultural land. In summer the weak positive influence of pine plantation in proximity to agricultural land on cat abundance suggests older pine plantations with larger trees may also provide shelter opportunities for the cats.

In this study cat population density was higher on the resource rich edges of farmland and lower in native forest where the preferred prey of cats was much lower. This is supported by Harper (2007) and Bengsen et al. (2016) who found home range size and population density varies greatly for cats in accordance with the availability of resources including prey and shelter (Bengsen et al., 2012). Cats in resource-poor habitats tend to have large ranges (up to 2324 ha in one study), while in more productive areas the density of cats is greater and home-range sizes are smaller. In Hawkes Bay, New Zealand, female cats had an average range of 86ha (Langham and Porter, 1991). Langham and Porter (1991) also found differences between nocturnal and day ranges and the degree of overlapping home ranges for both males and females (Langham and Porter, 1991) however this overlap reduced with lower resource levels (Konecny, 1987).

There are several explanations that may explain the negative relationship between the presence of cats and quolls in this study. For example, the results could be coincidence or may reflect a direct relationship. Other studies have identified differing requirements between the two species in vegetation structure for hunting, with quolls being better arboreally adapted than cats (Jones, 2003) giving rise to differing prey preferences. However they do overlap substantially in diet and require similar den and shelter sites (Glen and Dickman, 2008), and it is likely that either exploitation or interference competition may occur, especially during periods of resource limitation (e.g. drought, late winter). There is some suggestion of spatial separation occurring between the species with cats more prevalent on the edges of agricultural land and quolls in native forest.

4.3 Enhancing habitat values for quolls and devils

My findings suggest habitat for devils and quolls can be enhanced by introducing more structural complexity to simplified environments. This is of particular interest to plantation managers wishing to improve the quality of plantations as habitat for these two species. To encourage use of and breeding in proximity to plantations by quolls and devils, structural elements for use as denning sites could be added at the edges of the plantations, within streamside reserves, and other excluded areas, such as rocky knolls. Longer-term management actions to benefit quolls and devils could be directed at maintaining or encouraging vegetation diversity within the plantations through both mixed plantings and encouraging understorey species to benefit animal diversity.

Installation of artificial hollows for use by hollow dependent species, may compensate for a lack of hollows in plantation forests (Goldingay et al., 2015) and denning opportunities could be provided through retention of large woody debris following harvesting. Large organic matter within plantations will encourage greater biodiversity by providing media for saprophytic fungi, mosses and invertebrates which in turn will support insectivorous birds, reptiles and small mammals (Deal et al., 2017, Taylor et al., 2007, Lindenmayer et al., 2000).

There is also the potential to introduce more structural complexity into the forest as it grows (Carnus et al., 2006, Lindenmayer and Hobbs, 2004). The management of forests and plantations should be considered at a landscape scale to retain connectivity, including patches and riparian strips to encourage quolls and devils and prey species to move through fragmented landscapes (Jones and Davidson, 2016). Strategies to provide connectivity and diversity of habitats could include retaining existing areas of remnant native vegetation within plantation stands and replanting native vegetation corridors (Munks and McArthur, 2000, Jones and Davidson, 2016). This would promote an understorey comprised of native vegetation. Implementing mixed plantings would provide a mosaic of differing growth habits and ages for harvest. As cats prefer the edges of disturbed habitats, maintaining and encouraging understorey cover within plantations and around the forest edges may discourage both the exotic prey species and the cats that prey on them.

4.4 Study limitations

A limitation of this large survey is the amount of overlap between the designated landscape use categories as measured by the site-level parameters. This occurs because the site-level parameters are measured at a scale of a 5m radius around the camera sites, and the highly fragmented landscape means camera placement, particularly around ecotones, may not accurately reflect the dominant vegetation type in the vicinity. More robust factors for determining relationships between environmental attributes and landscape use by the target species are the proportions of each of the land uses (agricultural land, native grassland and moorland, native forest and plantation) around each site. If it were possible to measure and average the site-level attributes over the hectare surrounding the site, these factors might be more representative of the overall habitat and reveal stronger habitat relationships by and between the quolls, devils and cats.

Devil detection was influenced by the different bait recipes, with a higher likelihood of detection when using the main bait recipe (Bait 1). The recipes did not appear to be a factor for the detection of the other two species. Bait recipe was taken into account in the modelling and should not have changed the overall estimated abundance of devils. The difference in camera settings did not appear to influence the detection of any of the three target species.

The time since local disease outbreak (of DFTD), relative to the time the study was undertaken is likely to have affected the abundance and distribution of devils throughout the study area (Hawkins et al., 2006, McCallum et al., 2007). The disease has spread from east to west, and population decline follows in subsequent years (Hawkins et al., 2006). This is reflected in the occupancy and abundance of devils recorded on the cameras.

The results of this study at a site level within Tasmania should be relevant to determining habitat preferences for the abundance of quolls, devils and cats. The northwest of Tasmania where this study was undertaken is a high rainfall area with high topographic relief and is recognised as a core area for populations of quolls and devils, hence populations may be higher here, however the factors influencing abundance should remain constant. The results of other studies on habitat preference of quolls and cats on mainland Australia are consistent with my results, with quolls favouring more complex understorey while cats are more successful hunters where there is less complexity to provide refuge for prey (Glen and Dickman, 2006b, Glen and Dickman, 2011, Hohnen et al., 2016). Many of the native mesopredators globally are similarly reliant on structural complexity provided by the understorey and mature trees with hollows for hunting and denning (Potvin et al.,

2000, Gerber et al., 2012).

The effect of culling practices on the prey species (rabbits, pademelons, Bennett's wallabies, possums and wombats) by many landholders, was not assessed. This may be of relevance in determining whether there are thresholds in prey availability influencing the populations of the three predator species. In addition, there is likely to be some culling of cats, and some quolls and devils may be targeted as well. Further studies involving sites on private land should, where possible, canvas the landholder pest control practices.

At a few sites interference with the cameras by wildlife resulted in incomplete records of potential detections. Every effort was made to secure the cameras sufficiently to withstand investigation but cameras were on occasion knocked askew by animals. This may have influenced the number of detections but should have had little effect on the occupancy records for the target species.

4.5 Further research

The camera study successfully identified key factors within the variables considered that influence the abundance of the three target species, the quoll, devil and cat, in a heterogeneous landscape where the native vegetation is fragmented by agriculture and timber plantations. Studies of the habitats of predator species should take into account whether they are a generalist predator/scavenger, with the plasticity to change prey to take advantage of seasonal availability, or a specialist predator with a restricted range of available prey. Breeding and denning resources should also be considered within their niche requirements. These factors will undoubtedly influence predator tolerance to habitat change, loss and fragmentation. Other human-induced factors such as hunting, culling and the influence of domestic dogs on wildlife should also be taken into account (Pettorelli et al., 2010, Farris et al., 2017). Once the habitat requirements for each species are identified, there may be options available to improve the habitat for the most vulnerable of the species. Despite the devastating influence of the DFTD on the devils, from a habitat perspective the quoll appears most at risk from loss of prime forest habitat.

Further research is required into how devils and quolls function in plantations to provide an insight into resource requirements in this simplified environment. This study suggests quolls primarily use plantations with an open understorey for moving between areas, and these individuals are more likely to be males or sub-adults dispersing. Are quolls more likely to travel through plantations if the plantations are connected to native forest areas? If quolls are using some plantations for hunting, what prey are they eating? A dietary study would clarify whether the diet changes between the plantations and native forests. If there is a difference in targeted prey between native forest and

plantation, it may be due to a lack of habitat for the preferred prey, such as shelter, including tree hollows, understorey or windrow presence, absence or composition. If there is no difference in diet, then it would be more likely that the plantations lack the resources sought by the quolls themselves, such as structural complexity, shelter and denning sites. Devils appear to use plantations but it is not yet known how they are using them. For both devils and quolls, dietary and tracking studies would assist in determining any differences between the prey species use of plantations and native forest. Further analysis of data from this study would indicate if there are correlations between presence and abundance of prey with the predator species.

Cats appear predominantly to use plantations as an extension to their home range within agricultural land. A study could investigate how cats use plantations; whether cats are influenced by the prey species present or habitat factors such as variability in the understorey with clear areas interspersed with dense shrubbery. How does the cats' diet change when moving from agricultural land to plantation or native forest? How does size of the home range change between farmland and native forest? Is any change a result of less prey availability or lack of shelter and den sites?

While there have been trapping, tracking and camera studies on devils and quolls investigating the use of agricultural land in far northwest Tasmania (Andersen, 2016, Troy, 2014, Saunders, 2012), none have examined diet or denning in more intensively farmed areas. Linear features, such as tracks, fencelines, riparian vegetation and forest edges are used regularly (Andersen, 2016) and both species will investigate around buildings (pers. obs.), but the distances they will travel in the absence of cover and what their main prey species are in agricultural land has not been determined. Devils and quolls will use buildings for shelter and denning but the extent they make use of buildings, and the age, sex and breeding status of individuals using buildings has not been explored. The diet and prey resources on farms and around farm buildings, likewise, have not been investigated. Devils have a high dietary overlap with quolls (Andersen et al., 2016, Jones and Barmuta, 1998) which varies for both species with season and sex or size of the individuals. Devils have a greater component of their diet, particularly in summer, made up of large prey species than do the quolls. These prey species include wombats, macropods and possums but they will opportunistically include many smaller species and scavenged items. Dietary studies of quoll in forest and woodland habitats both in Tasmanian and mainland Australia, have found macropods, wombat, small mammal, bird, reptile and insect, common brushtail possum, common ringtail possum and greater glider (Belcher, 1995, Belcher et al., 2007, Andersen, 2016, Jones and Barmuta, 1998). Andersen (2016) found rabbits to be the largest component in the quoll diet in the Midlands of Tasmania, a drier agricultural region of the State. Quoll abundance was found to be positively influenced by rats *Rattus rattus*, commonly found in native forest in winter and the edges of agricultural land in both seasons

(Andersen et al., 2016). To what extent have rats become a prey species for quolls?

The study indicated there was a positive relationship between devils and quolls, and devils and cats, but a negative relationship between quolls and cats. Both devils and quolls were more abundant in native forest sites and this suggests there is either some dietary or temporal separation between devils and quolls. For cats too, there is likely to be either dietary or temporal differences with devils. It is unlikely devils would compete for dens with either cats or quolls, as they require substantially larger dens. Andersen (2016) found in her study in fragmented agricultural and coastal vegetation there was no spatial separation between quoll and devil denning sites, as den sites of an individual quoll and devil were only 400m apart. However, she did note temporal differences with quolls being more active in the early evening and morning prior to dawn, while devils were more active during the middle part of the night. Further research should investigate whether activity times are replicated in native forest and plantation.

With ample cover, cats are active both nocturnally and diurnally (Molsher, 2006, Harper, 2007) but, where there is human activity and limited cover, cats become more active nocturnally (Langham and Porter, 1991). This indicates behavioural plasticity where cats may also alter their activity times when faced with direct competition from devils or quolls. There is likely to be extensive dietary overlap between cats and quolls living in the same habitat, so the affinity of quolls for forests and cats for agricultural land may reduce direct competition between the species. As well, quolls are morphologically specialised for arboreal hunting, with an opposable clawless hallux on the hind feet and ridges on all foot pads (Jones, 2003), facilitating niche separation from cats and devils that may result in lower levels of direct competition between species.

Anecdotally, the distribution of pademelons and possums has changed markedly since the 1950s and 1960s. At that time, it was rare to see a pademelon north of Waratah, and encountering common brushtail possums was an exciting event as they were valued for their furs (T. Hayes, Pers. comm.). The most numerous prey species across all habitats in my study is the pademelon. They were detected at all sites but with varying abundance. Agricultural sites recorded the greatest numbers with pademelons using forest edges for refuge, emerging at dusk to browse on improved pastures. Agricultural sites were also highly favoured by the brushtail possums and black rats. With high productivity and little top down pressure from devils, numbers of these species have burgeoned. Native forest has the next highest abundance of prey species, including pademelons, possums, and rats. Species such as potoroos, bettongs and bandicoots were also more common on the interface with agricultural land but not consistently seen across sites. Landholder activities to control the numbers of herbivore browsers, by either fencing or culling should be studied for effectiveness, for

adverse effects on the native vegetation from over browsing and, in those areas where native predator numbers are high, for any limiting effects on the prey species numbers.

Plantations were variable in the numbers of the dominant prey species recorded. Further analysis of prey species abundance and availability in plantations, including the plantation conversion history, may suggest factors influencing their abundance. Percentage composition within the diet of devils and quolls would be of interest in gauging the dietary flexibility of devils and quolls in plantations, seasonally and at different stages of the breeding cycle. Surveys of devils and quolls in plantations would provide insight into the demography of plantation populations, including age-structure, sex ratio, and whether individuals are permanent residents or transient. Tracking movement patterns and fine-scale habitat use would assist in determining whether devils and quolls utilise plantations for denning, predation or merely as a component within their hunting range. A more thorough investigation is needed comparing potential den sites in plantations with potential den sites in adjacent native forest.

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